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LIFE HISTORY STUDIES AND THEIR RELATION TO PROBLEMS IN TAXONOMY OF DIGENETIC TREMATODES*

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For some years my students and I have been interested in digenetic trematodes from the standpoint of their life histories and also their taxonomy. I welcome, therefore, the opportunity to discuss before the Society the subject "Life history studies and their relation to problems in taxonomy of digenetic trematodes."

Although it would be of interest to review the many attempts to establish a system of classification for the Trematoda, time does not permit. It is sufficient for our purpose to call attention to certain systems. In 1858 Van Beneden divided the Trematoda into two groups, those which develop without a metamorphosis and those which develop with a metamorphosis. To the former he gave the name Monogenea (Monogénesès) and to the latter Digenea (Digénesès). He included in the Monogenea chiefly ectoparasites and in the Digenea endoparasites. This is the foundation of our present system.

A little more than three decades later Monticelli (1892) rejected this system of classification and developed one based on the organs of attachment. Although accepted by Maximilian Braun in his monumental work on trematodes (1893) and by others, Monticelli's system did not survive. Some aspects of that system as elaborated by Braun are of interest in connection with work to be discussed later. Braun divided the suborder Malacocotylea Monti. into two groups, Metastatica to include the Holostomidae, and Digenea *sensu strictu* to include the Amphistomidae, Distomidae, Didymozoonidae and Monostomidae. Braun also found it necessary to erect a special family, the Gasterostomidae, for the genus *Gasterostomum* and similar forms on the basis of their rhabdocoele-like gut, the arrangement of the genitalia and the excretory system, the special apparatus at the anterior end of the body and the peculiar form of the cercaria (*Bucephalus*).

That the Holostomidae = Strigeoidea were metastatic in development had been suggested by Leuckart (1889). This was based on the

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view, now known to be erroneous, that the miracidium in members of this family developed into the tetracotyliform larva directly, *i.e.*, without intervention of sporocyst or redial generations, and without the production of cercariae.

When Looss (1899) published his work on the trematode fauna of Egypt our knowledge of the systematics of digenetic trematodes was greatly advanced. This report contained the results of an investigation on the natural classification of the genus *Distomum*. His conclusions were based upon precise anatomical studies of adult worms. He erected many natural genera and 12 subfamilies. Many of the latter are now given familial rank.

Account must also be taken of the very significant contributions made by Odhner to the development of the modern taxonomic system of the DIGENEA. In a series of articles entitled "Zum natürlichen System der digenen Trematoden" and also in many other papers Odhner rendered a truly great service in reducing the great group of digenetic trematodes to an orderly system. In his work Odhner depended, as did Looss and many other investigators, on the detailed morphology of adult worms. He placed special emphasis upon the arrangement of the reproductive system, the excretory system and other anatomical structures in developing his ideas of relationship. Indeed, Odhner (1913: 313) appears to have coined the expression "the conservative nature of the excretory system" so much emphasized by later investigators.

Odhner (1905) divided the order DIGENEA into two suborders, GASTEROSTOMATA and PROSOSTOMATA, the former to include the genus *Gasterostomum* and other genera with non-perforate anterior suckers and rhabdocoele gut and the latter to contain all those remaining DIGENEA with perforate anterior suckers.

In the light of subsequent work involving life history studies certain of Odhner's conclusions as to relationships are of special interest. In his paper on the phylogeny of the *Bilharzia* = *Schistosoma* type he (1912) placed the blood fluke *Hapalotrema* Looss in the family HARMOSTOMIDAE because of an apparent resemblance morphologically to *Liolope copulans* Cohn, an intestinal fluke. He now proceeded to point out the connections of the schistosomes with the distomes through the series *Liolope*, *Hapalotrema*, *Bilharziella* = *Ornithobilharzia*, *Bilharzia* = *Schistosoma*.

In another paper (1913) he argued correctly on the basis of comparative morphology for the relationship between the genus *Cyathocotyle* and the HOLOSTOMIDAE = STRIGEOIDEA. In his analysis, however, he attempted to show that the holdfast organ peculiar to this group was homologous with the ventral sucker of the distomes and that the acetabulum of the holostomes was an accessory structure.

The attempts of Odhner and others to construct a taxonomic system on the basis of adult characters alone resulted in bringing together unrelated forms. It could not do otherwise in some instances because the development of certain organs used in comparative studies was unknown.

Information gained from studies of cercariae and of life histories was used as a tool in taxonomic work about as early as a sufficient body of data was available. During the nineteenth century a number of investigators rendered valuable service in describing the generations of digenetic trematodes in snails and in attempting to relate them to the adult worms. The discovery of the life history of the sheep liver fluke, *Fasciola hepatica,* by Leuckart (1882) and Thomas (1883) was an important contribution and led the way to the subsequent solution of other life histories. In 1909 Lühe published a classification of the cercariae. The solution of the life history of *Schistosoma japonicum* early in the second decade of this century and comparative studies upon cercariae brought valuable aid to the problems of taxonomy of trematodes.

Cort (1917) was the first to point out the importance of the excretory system as a basis for the establishment of a natural system of classification. He had made a comparative study of five fork-tailed cercariae, one of them *Schistosoma japonicum.* Two of the other cercariae lacked pharynges, two possessed them. The life history of *C. douthitti,* one of the apharyngeate cercariae, has been since worked out and found to be a schistosome. The two pharyngeate cercariae have since been proved by life history studies to belong to the STRIGEOIDEA. In spite of the differences in the matter of pharynges Cort stated, "The similarity of the excretory system, however, demonstrates their relationship to that family. These observations indicate the conservatism of the excretory system in trematodes and its value in establishing relationships in this group."

The work of Faust (1918, 1919, 1924), Sewell (1922), Szidat (1924) and of many others has amply established the correctness of this view. Faust (1919) developed the now well-known method of expressing the arrangement of the flame cells by means of a mathematical formula.

It will be recalled from an earlier part of this review that the strigeids had been considered to be metastatic in development. However, during the years 1920–24 three important investigations, namely those of Lutz (1920), Ruszkowski (1921) and Szidat (1924), proved conclusively that the strigeids are in fact true digenetic trematodes. They confirmed the earlier statements that the miracidium in this family possesses two pairs of flame cells and established the fact that the cercariae have forked tails with slender tail stems, that pharynges are present, and that the oral sucker bears no stylet. Szidat (1924) settled once for all that the holdfast organ peculiar to the strigeids arises from tissue posterior to the acetabulum and that the acetabulum in this group is homologous with the

ventral sucker of distomes. Their work made evident that the fork-tailed cercariae with pharynges described by Cort (1917) belong in fact to species of strigeids. Cort had claimed that the similarity of the excretory system to that of the schistosome cercariae demonstrates their relationship to the SCHISTOSOMATIDAE.

The study of La Rue (1926) on the relationships of the STRIGEIDAE was based directly upon the life-history studies of Cort, Sewell, Faust and others on the one side and of Lutz, Ruszkowski and Szidat on the other. To be sure, he had seen the miracidia, and had other information of a confirmative nature from life history studies carried on by his students. In that paper La Rue presented the conclusion that the STRIGEIDAE were related to the SCHISTOSOMATOIDEA. That statement was based not only upon the homology of the excretory system in the cercariae but also upon the fact that the miracidia of these two groups possess two pairs of flame cells while all other miracidia known at that time had one pair.

The researches of Hunter and Hunter (1934, 1935) showed that the miracidium of *Clinostomum marginatum* has two pairs of flame cells and that the ciliated epidermal plates are the same in number and arrangement as in the blood flukes and the strigeids. On this basis they pointed out the possibility of a relationship. The cercaria of this species was described by Krull (1934) as a fork-tailed cercaria with a long slender tail stem, a pharynx, penetration glands, a penetration organ like that of the schistosomes instead of the usual oral sucker. The excretory bladder is V-shaped as in schistosomes and strigeids and the flame cell pattern is also similar. The results of these studies indicate that the CLINOSTOMIDAE must be placed in the group containing the STRIGEOIDEA and the SCHISTOSOMATOIDEA.

What now can be said for the claim put forth by La Rue (1926) that probably the BUCEPHALIDAE are related to the strigeids and the schistosomes? That claim was based on the morphology of the adults and the cercariae as described in the literature. The miracidium was at that time unknown. The researches of Woodhead (1929, 1930) failed to furnish information on the flame cells in the miracidium and gave little support to the claim for relationship. In this case the Scotch verdict "not proved" is in order.

In the discussion thus far the validity of the excretory system as a criterion of relationship has been assumed as proven. However, in 1929 Stunkard carefully compared the excretory systems of *Heterophyes*, *Microphallus* and *Cryptocotyle* especially with respect to the flame cell formulae. At the time of writing, these three genera were commonly conceded to belong in the family HETEROPHYIDAE. Stunkard pointed out that "the excretory systems in the three genera are strikingly different. The form of the vesicle of Microphallus is much like that of Heterophyes

but the common collecting ducts are very short in Microphallus whereas in Heterophyes they extend one-half of the length of the body." There were other differences. He also showed that the excretory pattern of *Microphallus* more closely resembles that of *Heterophyes* than the latter resembles *Cryptocotyle*. As a result of this careful study he concluded: "The striking differences in the excretory systems and flame cell formulae of genera, admittedly closely related, are subversive to the thesis that the excretory system affords the only certain basis for determining genetic relationships among the trematodes and show the need for caution in the formulation of such sweeping statements."

Stunkard's word of caution is well taken and should be heeded in all future work. The value of his caution, in my opinion, is not minimized by the conclusions of Rothschild (1937) that the MICROPHALLINAE develop from xiphidiocercariae of the "Ubiquita" group and therefore must be withdrawn from the HETEROPHYIDAE which, as is well known, have cercariae of a very different type.

In a recent classification (that of Faust, 1932) the superfamily HETEROPHYOIDEA is listed as containing three families, viz., HETEROPHYIDAE, MICROPHALLIDAE and LECITHODENDRIIDAE. The case for MICROPHALLIDAE has already been stated. For the LECITHODENDRIIDAE McMullen (1936) has shown that in *Mosesia chordeilesia* the cercaria is a xiphidiocercaria with a ventral sucker. Relationships for these two families must therefore be sought elsewhere, perhaps with the PLAGIORCHIIDAE among whose species many life histories have been studied during the last few years.

If form of cercaria is of any significance in establishing relationships within and between families, and we believe it is, then attention must be called to the possibilities of relationships between the HETEROPHYIDAE and the OPISTHORCHIIDAE. This indeed has been done by Witenberg (1929) who placed these two families in the superfamily OPISTHORCHOIDEA. For the HETEROPHYIDAE the cercarial form is of the "pleurolophocerca" type of Sewell. In this type the ventral sucker is lacking while in the closely similar cercariae of *Opisthorchis felineus* as determined by Vogel (1934) and of *Clonorchis sinensis* by Faust and Khaw (1927) the cercariae possess ventral suckers. While the flame cell patterns are different the resemblances are such as to point to a relationship within a superfamily. In support of this view I may mention the fact that in a recent study in my laboratory my former student, Dr. Ameel (unpublished research), was unable to determine from a morphological study whether a certain cercaria was a heterophyid or an opisthorchid until the metacercaria had developed.

Lacking information on life histories considerable emphasis has been placed on the form of the excretory vesicle as an important taxonomic

character. Among others Baer (1924) and Mehra (1931) expressed this view. The principal types of excretory vesicle are cylindrical, Y-shaped and V-shaped; sometimes to these a fourth is added, namely the network type of excretory system.

If information on life history is lacking can it be assumed that the excretory system of the adult has retained its original form? After a survey one of my students (Wu, unpublished research) concluded that the vesicle remained unchanged in species of PLAGIORCHIIDAE, SCHISTOSOMATIDAE, and BUCEPHALIDAE, but that it undergoes profound changes in species of STRIGEOIDEA and in *Fasciola hepatica* and in certain other trematodes.

The character of the change in the excretory system of STRIGEOIDEA can be illustrated by changes that occur in *Alaria mustelae* as described by Bosma (1934). In that species the original V-shaped bladder becomes doubled and a new set of main ducts and anastomosing branches comprising the reserve excretory system develop as an outgrowth from the original lateral ducts. In *Fasciola hepatica* the original excretory vesicle in cercaria and metacercaria is plainly "Y"-shaped but in the adult a branch extends forward between the slender forks of the vesicle. Numerous branches arise from the long stem and forks of the "Y." These anastomose throughout the entire post-acetabular region of the body. Because of these anastomoses the forks and the branch between them are inconspicuous and the entire excretory system has the appearance of a network (Wu, unpublished research). It is to be noted that the original form of the vesicle was plainly Y-shaped. Shall other trematodes having an anastomosing or network type of excretory system be placed with *Fasciola* because of this character?

The relationships of the three main forms of excretory systems have been brought together by McMullen (1937) in the form of a plate. It is evident that modifications in the length of stem may change the "Y"-form to the "V"-form, while extent of dilation of the branches may determine whether the form shall assume the Y-form or the cylindrical.

Further modifications of the excretory vesicle may occur through proliferation of tissue or other changes in that part of the bladder which is formed by invagination from the dorsal side of the body. A change of this kind occurs in *Macrovestibulum eversum* Hsu (1937). In that species the invaginated tissue continues to proliferate laterally and into these masses of cells a lumen is formed continuous with the bladder. These lateral extensions of the bladder are muscular, lined with cuticula and eversible through the excretory pore. Are modifications of this kind significant in taxonomy? In my opinion they should have no more than generic significance at the most.

Concerning the taxonomic value of the form of the excretory vesicle in the adult, it is probably safe to say that its value depends upon its retention of its original form, that is, its form in the cercaria, or upon the investigator's ability to determine what that original form was. In the absence of a knowledge of the life history of the species this may be impossible.

Before leaving the subject of the excretory system allow me to call attention to the need for more information on the method of formation of the excretory vesicle in digenetic trematodes. Sinitsin (1911) showed that the vesicle was formed in two ways, the one by a fusion of the original pair of ducts which at first discharge separately to the exterior in the postero-lateral parts of the body of the developing cercaria. In the other method an invagination of the postero-dorsal part of the body comes into contact with the pair of ducts, fusion occurs and discharge now occurs through this new vesicle with its dorsal pore. The first method of vesicle-formation occurs in the fork-tailed cercariae and in some others. The second occurs in some of the stylet cercariae.

Of the two methods of vesicle formation the first mentioned, that of fusion of the two lateral ducts, appears to be the most primitive. Evidence for this is found in such species as *Macrovestibulum* in which this type of excretory vesicle with discharge through ducts in the tail is first established, then the second method is superimposed on the first and the ducts in the tail lose their connections with the exterior.

An examination of figures of cercariae indicates that a similar process apparently occurs in many of the stylet cercariae, in the pleurolophocercariae of the HETEROPHYIDAE and possibly in those of the OPISTHORCHIIDAE, although the evidence is not clear in these. The published figures of echinostome and amphistome cercariae leave the reviewer in considerable confusion. Some of them show only the two openings in the tail, others show these and another opening dorsal to the bladder. Some of the figures of stylet cercariae show a central duct in the tail without openings to the surface and an opening dorsal to the excretory bladder. From certain work in progress by my students there is reason to believe that these latter figures are correct. It is evident that much more information is needed on the process of formation of the excretory vesicle. With a large mass of data on this process it might be possible to determine whether it is of significance in the development of a natural system of taxonomy. We seriously need a considerable series of studies on trematode embryology. Much of our present work on life histories and on the cercariae is done without a knowledge of trematode embryology and this leads to misinterpretation.

The many studies on cercariae and of entire trematode life histories have made it increasingly evident that organs of attachment are not good characters for the establishment of families or suborders. Odhner

(1911*a*) on the basis of comparative anatomical studies alone concluded that "the monostomes of the family Angiodictyidae are Amphistomes which have lost their posterior suckers." The cercariae of the *"Ubiquita"* group of Sewell are monostome-styleted cercariae which according to Rothschild (1937) develop into distomes of the subfamily MICROPHALLINAE. The cercaria of *Clinostomum marginatum* likewise lacks a ventral sucker but the latter develops during the long metacercarial period. A survey of the adult blood flukes shows that many are distomate, others monostomate, while others have no suckers. Certain strigeids also have no acetabulum.

That certain of the monostomes have been derived from distomes through reduction and loss of the acetabulum was believed to be true by Cohn and Odhner. This is supported by Stunkard (1934) who found that the cercaria of *Typhlocoelum cymbium* of the family CYCLOCOELIDAE has an acetabulum while the adult has none. Doubtless other similar examples could be marshalled to show that little dependence can be placed on the suckers as characters for the higher taxonomic ranks.

The pharynx according to Miller (1926) is a character of considerable value. Its absence characterizes the entire group of bloodflukes, both adults and cercariae. Its presence characterizes the STRIGEOIDEA. It would be most convenient here to pass hurriedly by the genus *Apharyngostrigea* which apparently has no pharynx. Since the life history is not known, it is impossible to determine whether the cercariae in this genus possess pharynges. Can the pharynx degenerate during the metacercarial stage? To this question we do not, to my knowledge, have the answer.

Enough information is now available with respect to the intestinal branches to conclude that their length or other variations in structure have little more than specific or generic value at the most. This also may be said of connections of the intestinal branches to the exterior directly through one or more ani or through the excretory system. On this matter Stunkard (1931) who made an extensive survey wrote: "Recent investigations have shown that the intestinal ceca communicate with the exterior in a large number of digenetic trematodes. The connection may be by way of the excretory vesicle; there may be a single, separate opening; or there may be two anal pores. It appears that such a connection has developed independently in several different families. . . . Another interesting fact is that communication with the exterior is not uniformly present in all members of those families in which it occurs, and consequently the conclusion is drawn that it is a relatively recent acquisition, developed in certain families after they had become differentiated and established as definite groups. . . . Since schemes of classification are arbitrary and somewhat graphic means of representing phylogenetic rela-

tions, it appears that the presence or absence of secondary connections between the alimentary tract and the exterior is not a character of great taxonomic importance in the digenetic trematodes."

In summarizing we may conclude that the development of a natural taxonomic system for the DIGENEA must be based upon comparative anatomy of all stages in the life history.

Account must in many cases be taken of the miracidium, especially of its flame cells and possibly of the number and arrangement of the epidermal plates.

In the cercaria attention must be given first to the form or type of the cercaria. Type of cercaria usually takes penetration apparatus into account as well as tail and other external characters. It seems probable that our classification of the cercariae should now be revised in the light of recent advances of our knowledge.

Of special importance in the cercaria are the pharynx and the characters of the excretory system including flame cell pattern, form and proportions of the excretory vesicle. Possibly the method of formation of the excretory vesicle and the excretory pore may have value as characters.

In the adult stage consideration must be given to the arrangement of the reproductive organs, but little value should be attached to the suckers as characters for ranks as high as family and superfamily. Openings of the intestinal branches have no more than generic value, and not always that.

May I express the conviction that our knowledge is yet far too fragmentary to present anything like a finished taxonomic system for the DIGENEA that will express genetic relationships. Much progress has been made during the last few decades. Further progress awaits more knowledge, particularly of the life history stages including embryology.

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THE SUCKING LICE OF AMERICAN MONKEYS

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INTRODUCTION

Some years ago (1926) the writer published a revision of the American lice of the genus *Pediculus* which contained a synopsis of the species found on various American monkeys. Although the amount of material available from our monkeys at that time was small, yet it was sufficient to demonstrate that these lice were, in nearly all instances, distinct from those normally infesting man, and that more than one species was concerned.

Up to that time much doubt had existed as to the specific distinctness of any of these lice found on American monkeys. Even no less an authority than G. H. F. Nuttall (1919, 1920) then Quick Professor of Biology at Cambridge University, England, asserted that such lice represented no more than a race of *Pediculus humanus*.

In recent years the writer has availed himself of every opportunity to acquire and study lice from American monkeys with the result that it is believed the National Museum collection of these forms can not be equaled elsewhere. The credit for bringing together such a collection should go largely to certain individuals who have either sent in material or notified the writer of its presence. Particularly is he under obligation to Dr. W. M. Mann, Director of the National Zoological Park, and to Gerrit S. Miller, Jr., Curator of the Division of Mammals, U. S. National Museum. Dr. Mann not only has helped the writer in various ways to obtain material but some years ago assigned to him a desk and laboratory space at the zoological park so that much work with lice could be done at the park grounds.

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Nuttall (1919, 1920) regarded all lice from American monkeys as *Pediculus humanus,* yet when Ferris (1935) studied the Nuttall collection he came to a very different conclusion. Ferris (1935) regards them as different from *P. humanus.* However, like Professor Nuttall, to whom he dedicates his recent work, he decides that all of the true monkey-infesting forms are alike and places them in a single species. Unfortunately Professor Ferris did not examine the types of two of the four species, and does not go into the consideration of geographical races.

The confusion existing in regard to the identity and taxonomy of the sucking lice of American monkeys is the result of one or more of the following factors:

1. Inadequate technique in the preparation of material for study.
2. The utilization by nearly all workers of characters that do not really differentiate a species in this group.
3. The difficulty existing in getting preparations of the laterotergites so as to show them unstained, in lateral view and without distortion.
4. The omission of descriptions of the eggs, which possess valuable taxonomic characters.
5. The lack of knowledge as to the source of the louse material or the locality from which the host came.
6. The transfer of louse species to unnatural hosts in cages where monkeys of different species are mixed.
7. The large amount of temporary straggling on both live and dead hosts at zoological parks,—institutions from which much of the material has come.
8. The lack of biological studies on the different forms, particularly in regard to the possible transfer to, and permanent infestation of, one host by lice from another, and in regard to possible hybridization between the different forms of lice.

The terminology employed in the present paper has been reviewed by R. E. Snodgrass of the Bureau of Entomology and Plant Quarantine. It is particularly important to note that for the first time the present writer (following Snodgrass) has introduced the term laterotergite to take the place of paratergal plate in the literature dealing with the *Anoplura.* The two terms are entirely equivalent.

THE TAXONOMIC VALUE OF EGG CHARACTERS IN THE GENUS *Pediculus*

The shape and size of the egg (Fig. 1) and of the cement cup which attaches the egg to a hair of the host have been used to a very limited degree in the differentiation of subgenera and species in the genus *Pediculus* (Ewing, 1933). The extent of individual variation of the egg itself, either in size or shape, is not great; however, the shape is modified considerably by the various methods of treatment employed in mounting the

eggs on microscope slides. The importance of the shape of the cement cup as a specific character in *Pediculus* has been emphasized by Hinman (1931). Let us investigate its possibilities further.

In order properly to appraise the taxonomic value of the characters of the cement cup of the egg in *Pediculus,* it is very important to observe whether or not important changes occur in the shape of this cup when the eggs are attached to different types of hairs, and more particularly when eggs of one louse species are laid on hairs of different host species.

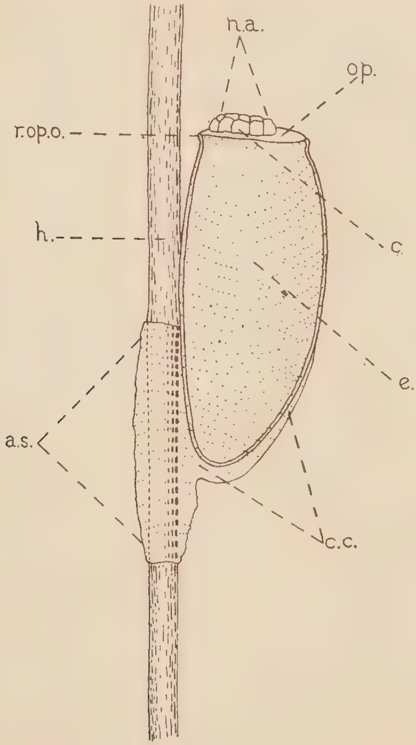

FIG. 1.—Egg of *Pediculus humanus americanus,* from scalp of Peruvian Indian mummy, ×75; *a.s.,* attachment sheath of cement cup; *c.,* cellula; *c.c.* cement cup; *e.,* egg; *h.,* hair; *n.a.,* nodular area; *op.,* operculum; *r.op.o.,* rim of opercular opening.

When an egg is attached to two or more hairs, or to the attachment sheath of another egg, or to the fabric of a garment, the attachment sheath of the cup is quite naturally abnormal. In the body louse of man the cement that would usually form a sheath about a hair may be so spread about when the egg is attached to the fabric of clothing that no real sheath is formed.

An examination of the eggs of *P. atelophilus* and of *P. chapini* on the hairs of an individual host shows that, in both species, variations in the

shape of the cement cup, particularly that of the attachment sheath, are independent of the size of the hair to which the eggs are attached. Eggs on hairs of the same size are found to have either long or short sheaths, but always within a certain range depending on the species of louse concerned. Further, the writer has observed that frequently almost the extreme range in the variation of length of the attachment sheath is to be found between adjacent eggs on a single hair! This fact alone indicates that most of the variation in the attachment sheath is independent of the size or shape of the hair to which it is attached. Thus it is possible to utilize the characters of the cement cup in identifying the eggs of a given species of *Pediculus,* regardless of the size or shape of the hairs to which they are attached. Also, the specific relationships of the cement cups usually can be determined, regardless of the host upon which the eggs are laid.

THE TAXONOMIC VALUE OF CERTAIN NYMPHAL CHARACTERS IN *Pediculus*

Only in one species of monkey-infesting lice of the genus *Pediculus* was the writer able to get a complete series of nymphs. This species was *Pediculus atelophilus.* The first nymph, or protonymph (Fig. 2, *a*), was reared from eggs obtained from an infested adult female spider monkey, *Ateles geoffroyi,* at the National Zoological Park. This monkey not only allowed the writer to pull out egg-bearing hairs from her furry coat, but appeared to enjoy the procedure immensely. She would press forward eagerly on the writer's approach to her cage and at once present herself for the hair-pulling process.

The last, or third, stage nymphs (Fig. 2, *c*) were identified without rearing, by finding mounted nymphal specimens with adult individuals in the process of formation inside of the nymphal skins. Having determined the first and third nymphs, the second nymphs (Fig. 2, *b*) were identified by comparison with these two.

The major differences between the three nymphal instars of *Pediculus atelophilus* (described farther on under the heading, "Description of Species") are the same as those between the nymphal instars of *Pediculus humanus* Linnaeus (Keilin and Nuttall, 1930). Like *P. humanus* the first nymph is pale and poorly sclerotized; the last three antennal segments are indistinctly separated; the abdomen is relatively much smaller in proportion to the rest of the body than in later stages; the laterotergites are absent, and the chaetotaxy of the abdomen is characteristic. The chief differences between the three nymphal instars are to be found in the chaetotaxy of the abdomen and structure of the laterotergites.

Only in the case of third nymphs has the writer been able to get a series of the same nymphal stage for different species of *Pediculus.* Third nymphs are at hand for the following species and varieties:

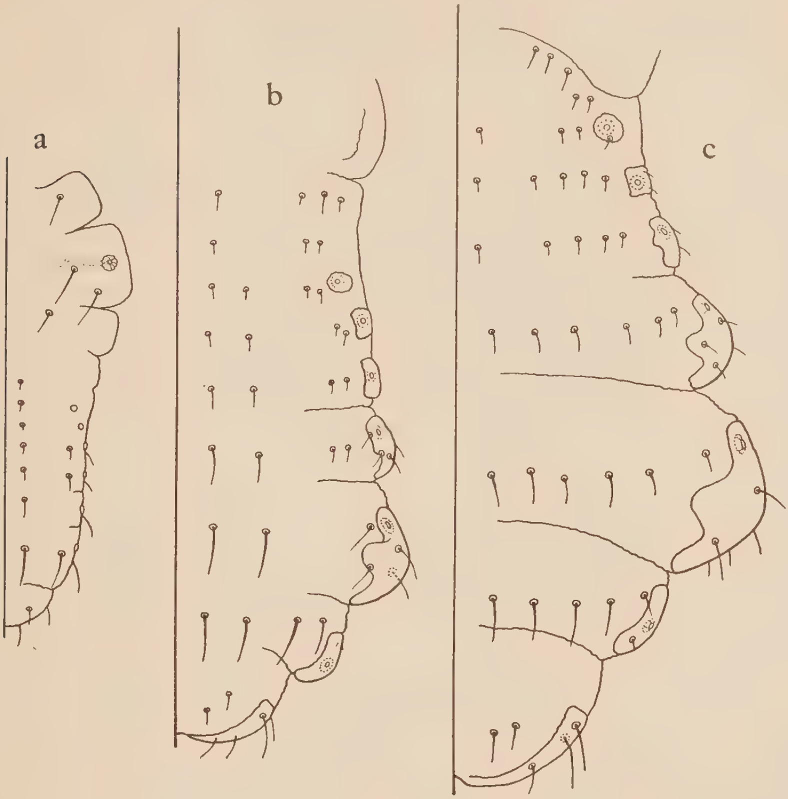

FIG. 2.—The three nymphs of *Pediculus* (*Parapediculus*) *atelophilus* Ewing; *a*, dorsal view of right half of body of first nymph; *b*, dorsal view of right half of abdomen of second nymph; *c*, dorsal view of right half of abdomen of third nymph. All drawings, ×75.

Pediculus humanus capitus from man.

Pediculus humanus corporis from man.

Pediculus humanus americanus from pre-Columbian Indian mummies.

Pediculus pseudohumanus from two species of monkeys from the upper Amazon.

Pediculus atelophilus from a Guatemalan spider monkey.

Pediculus chapini from a South American spider monkey.

Pediculus lobatus from a Bolivian marmoset.

Pediculus simiae from a chimpanzee.

When the third nymph of each of these forms is compared with the adult of its own species the following basic differences are noted:

1. It is smaller.

2. The dorsal abdominal setae are fewer and are always arranged in a single transverse row on each segment.

3. The laterotergites are usually differently shaped and smaller.
4. No external sexual characters are present.

When the third nymph of one species or one variety is compared with that of another species or variety some striking results are obtained. In general if the adults of one species are very similar to the adults of another, the third nymphs will have about the same degree of similarity as these adults. But sometimes the third nymphs of two related species differ more from each other than the adults of these two species, and sometimes they are more similar than the adults.

The characters that have been used to distinguish one nymphal instar from another in a single *Pediculus* species, are the same ones that are most useful in differentiating the third nymphs of different *Pediculus* species. These characters have to do with the chaetotaxy of the abdomen and the structure of the laterotergites.

THE SUBGENERA OF *Pediculus*

The present writer has divided *Pediculus* into three subgenera: *Pediculus,* for the man-infesting varieties (or species), which are practically world-wide in distribution; *Parapediculus* (Ewing, 1926) for the New World species found on monkeys and *Paenipediculus* (Ewing, 1932) for the African species on the chimpanzee.

As already pointed out (Ewing, 1933) *Paenipediculus* differs sharply from *Pediculus* in the following stages: Egg, first nymph and adult. It is now apparent that equally important differences exist in the third nymphal stage. Such adult characters of the subgenus *Paenipediculus* as the following may well be considered of generic importance: anterior pair of legs distinctly longer than others; abdomen not distinctly demarcated from thorax and with sides subparallel anterior to segment VI; laterotergites I to III vestigial, ringlike; abdominal setae minute and arranged in transverse rows, there being typically a single row to an abdominal segment.

Further study may justify the raising of the subgenus *Paenipediculus* to the full status of a genus.

With *Parapediculus* conditions are different. The writer's study of *Pediculus pseudohumanus* indicates very strongly that this species so connects *Parapediculus* with *Pediculus* that there appears to be some justification for suppressing the former subgenus. Yet a study of the eggs and nymphal characters of all the species of the genus *Pediculus* indicates, in a way, a basic relationship of *Parapediculus* to the chimpanzee louse and *Paenipediculus.*

This relationship is indicated in the eggs of *Parapediculus* species which show a strong tendency to become constricted near the attachment end and for this constricted end to be curved toward the attached hair.

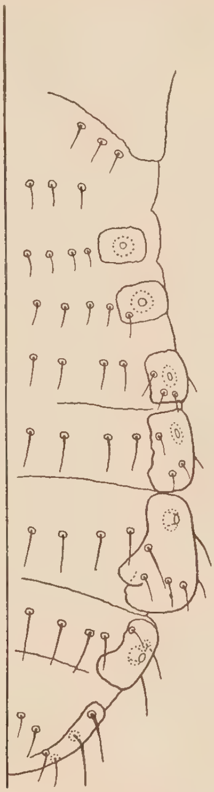

FIG. 3.—Dorsal view of right side of abdomen of third nymph of *Pediculus* (*Parapediculus*) *pseudohumanus*, new species, ×75.

This tendency is particularly pronounced in the eggs of *P. atelophilus* (Fig. 5, *b*). And the eggs of this species approach those of the chimpanzee louse, *Pediculus simiae* Ewing, in two other respects, the swollen condition of the egg near its middle and the reduction of the nodular area of the operculum.

A basic relationship of *Parapediculus* species to the chimpanzee louse and the subgenus *Paenipediculus* is further indicated in studying the third nymphs of all *Pediculus* species and varieties. In the third nymphs of the subgenus *Pediculus* the first three laterotergites are large and of about the same size as the fourth laterotergite; the fifth laterotergite is but slightly enlarged, slightly cupped, and usually is without lobes; the dorsal abdominal setae on the typical segments are almost subequal and are arranged in eight longitudinal rows and in transverse rows (one row to a segment). In the third nymph of *Paenipediculus* conditions are very different: The first three laterotergites are vestigial rings; the fifth laterotergite is greatly enlarged, extremely cupped and strongly lobed;

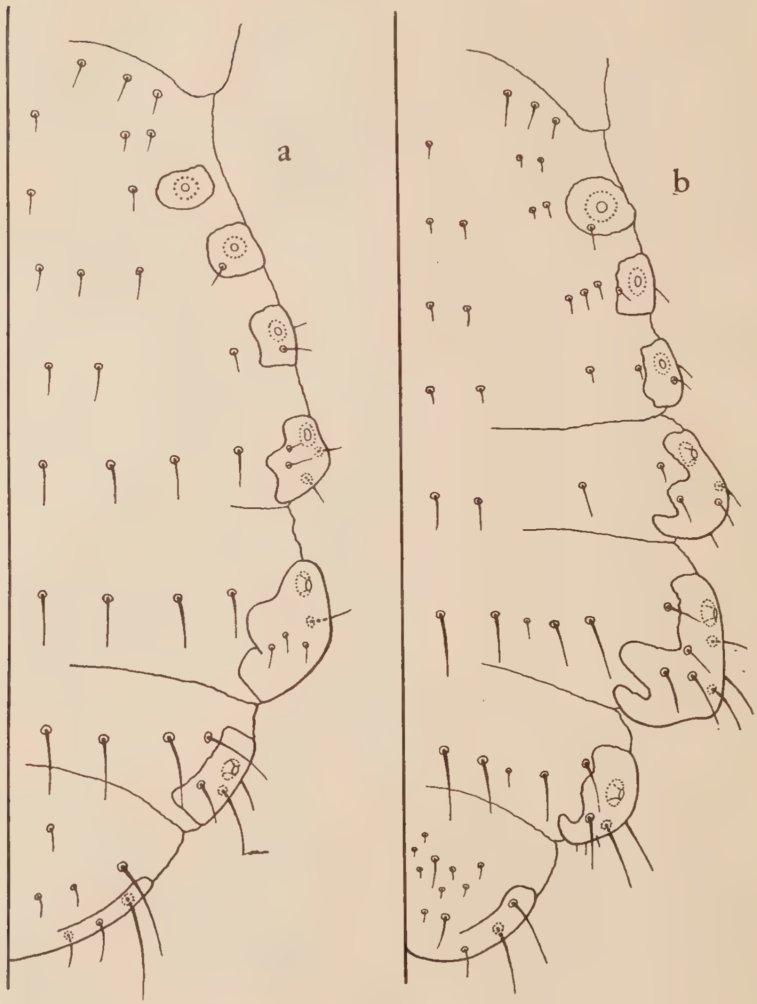

FIG. 4.—Dorsal views of right side of abdomen of third nymph of *a, Pediculus* (*Parapediculus*) *chapini* Ewing and *b, Pediculus* (*Parapediculus*) *lobatus* Fahrenholz. Both, ×75.

the dorsal setae are absent from the first five abdominal segments, six and seven bear a single pair each, while the eighth segment has only six setae arranged in a transverse row.

When the third nymphs of *Parapediculus* species are compared with those of *Pediculus* and *Paenipediculus* in regard to the characters just given, it is noted that an intermediate condition exists in every species. The third nymph of *pseudohumanus* is very close to that of *Pediculus humanus,* while that of *lobatus* shows very strongly an approach to the

third nymph of *Paenipediculus simiae* in the reduction in size of the first three laterotergites, the increase in size and in degree of cupping of the lobes of the fifth laterotergite, and the reduction in size and number of the dorsal setae of the first six abdominal segments.

Finally it should be emphasized that while the egg and third nymph of *Parapediculus lobatus* very definitely approach those of *Paenipediculus simiae* in certain respects, there is a vast difference between the two species in the characters of the adults.

For the present it appears to the writer that *Parapediculus* should be retained as a subgenus, while there might be justification for the raising of *Paenipediculus* to the status of a genus.

THE STATUS OF *Pediculus quadrumanus* (MURRAY) (1877)

Murray (1877) was the first to describe a *Pediculus* species from an American monkey, using the name *Haematopinus quadrumanus.* Hence, if all the forms of this genus occurring on American monkeys are to be regarded as varieties of a single species, this species probably should take the name of *Pediculus quadrumanus* (Murray). That Murray's *quadrumanus* was a *Pediculus* is clear enough, but it may have been only one of the man-infesting varieties of *Pediculus humanus* occurring on a species of *Ateles* as a straggler. However, such cases of straggling on *Ateles* must be very rare. Out of a total of twenty-two different lots of specimens that the writer has taken from live or dead monkeys of the genus *Ateles* or from their skins he has found among them not one specimen of *humanus.*

THE *Pediculus consobrinus* OF PIAGET (1880)

Piaget (1880) questionably described as new, under the name of *Pediculus consobrinus,* a louse taken from a spider monkey, *Ateles pentadactylus.* He gave a good figure of this louse which indicates (but of course does not prove) that the specimen (or specimens) from which the figure was made was a true monkey louse. Ferris (1935), however, obtained a single female of *Pediculus consobrinus* (all that remained) from the old Piaget collection of lice, and has redescribed and figured it showing that this specimen evidently is only *Pediculus humanus.* It appears, therefore, since both Piaget and Ferris have given very good drawings that they must have figured specimens belonging to different species. In other words, Piaget apparently had specimens that belonged to two species, one being a true monkey-infesting louse and the other *Pediculus humanus.*

If the single remaining specimen from the old Piaget collection, which was described by Ferris, is to be regarded as the type of Piaget's species, *Pediculus consobrinus* becomes a synonym of *Pediculus humanus*

Linnaeus. It is so regarded by Ferris. It is interesting to note in this connection that Piaget has figured the dorsal abdominal setae of his *Pediculus consobrinus* arranged correctly in transverse rows as they are in true monkey-infesting species, while Ferris (1935) does not represent them thus in his drawing of a monkey-infesting species, although these setae had been correctly figured by Hinman as late as 1931 for *Pediculus atelophilus* Ewing, an *Ateles*-infesting species.

THE *Pediculus affinis* OF MJÖBERG (1910)

Mjöberg (1910) described as *Pediculus affinis* a louse which was questionably taken from "*Ateles* ape" in a traveling menagerie. He considered it very close to *Pediculus consobrinus* Piaget but stated that it differed from Piaget's species especially in the length of the second antennal segment, the stronger lobing of the last abdominal segment, the shape of the genital plate and the gonopods. The writer has failed to find that these characters are of value in the differentiation of the species of *Pediculus* occurring on monkeys. Further, it is noted that Mjöberg's figure of the egg of *P. affinis* does not agree with any of the known forms occurring on species of *Ateles*. It does represent, however, very well the egg of *Pediculus humanus*. Also the drawing given of the last segment of the abdomen agrees very nicely with certain forms of *Pediculus* occurring on man. For these reasons *P. affinis* is regarded as only a variety of *Pediculus humanus*.

THE *Pediculus mjöbergi* OF FERRIS (1916)

Ferris (1916) proposed a new name for *Pediculus affinis* Mjöberg, the name *Pediculus affinis* having been previously used by Burmeister for a louse now placed in the genus *Polyplax*. Since Mjöberg's species is to be regarded as a variety of *Pediculus humanus* as just shown, the *Pediculus mjöbergi* of Ferris also takes the same status.

DESCRIPTION OF SPECIES

In presenting the descriptions of the different stages and the two sexes of the four species of *Pediculus* found on American monkeys the writer has attempted to confine his remarks strictly to those characters of value in taxonomic differentiation. In nearly all of the taxonomic literature dealing with the genus *Pediculus* there has been included an amazingly large amount of descriptive matter that can only confuse the taxonomists since it deals obviously with characters that have no taxonomic value. Some workers even up to the very present insist on befogging the whole problem by going into descriptive detail of characters that are plainly due to faulty technique, individual variation, hybridization or a state of repletion following feeding.

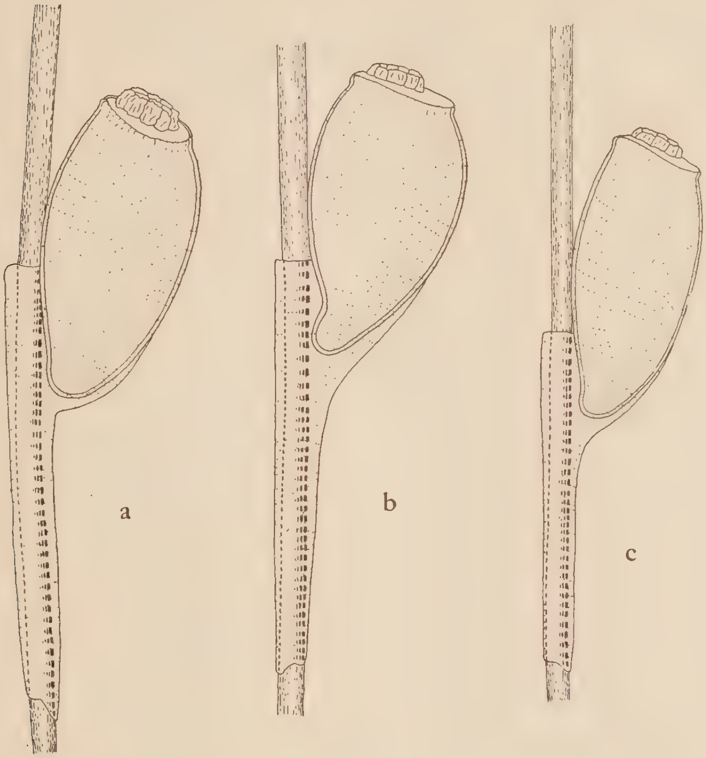

Fig. 5.—Eggs of three species of *Pediculus* (*Parapediculus*): *a*, of *P.* (*P.*) *pseudohumanus*, new species; *b*, of *P.* (*P.*) *atelophilus* Ewing; *c*, of *P.* (*P.*) *chapini* Ewing. All × 50.

Pediculus (*Parapediculus*) *pseudohumanus* n. sp.

(Fig. 3; Fig. 5, *a*; Fig. 6, *a*)

Female.—Body setae slightly peglike. Dorsal setae of each typical abdominal segment arranged for the most part in three irregular transverse rows, the setae of the middle row being somewhat longer than those of the other two rows. Abdomen rarely greatly distended. Laterotergites long, well pigmented, and those of typical segments almost as long as laterotergal area. Laterotergites as follows: I subrectangular, broader than long, and occupying about one-half length of laterotergal area; II almost twice as long as I, but no broader; III much larger than II, nearly as long as laterotergal area and with small lateral lobes situated almost at posterolateral angles; IV similar to III but larger; V longest of all laterotergites, oval, without lobes, and with spiracle situated slightly in front of center; VI small, subrectangular, without lobes, about one-half as long as V, and occupying a little more than one-half length of laterotergal area. Setae on laterotergites rather numerous, there being about 20 on laterotergite V.

Total length of body of female, 3.100 mm; width, 0.975 mm.

Male.—With the usual differences between male and female and in addition: Dorsal setae fewer and smaller in first and third transverse rows of typical abdominal segments, also differing from female in presence of small tergites and

sternites, each of which may be divided into two small transverse bars. Laterotergite I different from that of female, being smaller and very irregular in shape. Genital armature the same as in other monkey-infesting species of *Pediculus*.

Total length of body of male, 2.250 mm; width, 0.735 mm.

Egg.—Sides of egg next to and away from hair slightly and about equally rounded, base very slightly constricted and slightly turned toward hair, also frequently bearing a small tubercle. Nodular area of operculum composed of 7 to 8 peripheral cellulae, 1 to 2 central cellulae, and occupying about two-thirds of diameter of operculum. Edge of egg shell next to opercular opening cupped inward. Wall of cement cup next to hair very thin, being much thinner than average thickness of wall away from hair. Attachment sheath thin-walled and with very long lower end, in some specimens this sheath greatly exceeds egg itself in length.

Length of egg, 0.905 mm; greatest width, 0.460 mm. Shortest attachment sheath measured, 1.110 mm; longest, 1.240 mm; average for 6, 1.165 mm.

Third Nymph.—Along front margin of abdomen, on each side, three subequal dorsal setae. Slightly behind these setae, on each side, three similar subequal setae. Dorsal abdominal setae only slightly increasing in size from second to eighth segment; arranged in complete transverse rows on segments III to VIII, there being eight setae in each row. Laterotergites as follows: I about equal to II, only slightly oval in shape and broader than long; II smaller than III, subrectangular, broader than long; III an irregular square with spiracle in middle; IV much larger than III, occupying most of laterotergal area; V largest of laterotergites, slightly cupped, with rather small lobes; VI about the same size as IV, much broadened at posterior end, without lobes.

Total length of body, 1.515 mm; width, 0.530 mm.

The mounted nymphs of this species at hand are not engorged, and are slightly shriveled by the mounting medium. The drawing was made from such an unengorged specimen.

Type host.—*Pithecia monachus*.

Type locality.—Type specimens taken from a saki monkey that died at the National Zoological Park, Washington, District of Columbia. Original home of type host is the Upper Amazon.

Type slides.—U.S.N.M. No. 51451.

Remarks.—Material examined as follows: Many males and females and a few third nymphs and eggs from type host (U.S.N.M. 255542), at Washington, District of Columbia, August 29, 1930, by H. E. Ewing; many males and females and several eggs from a monkey, *Cacajao rubicundus*, coming from the Upper Amazon, that died at the National Zoological Park, Washington, September 10, 1930, by H. E. Ewing; three males, four females and one nymph from an Indian woman, Coban, Guatemala.

The specimens upon which this description is made were questionably identified (Ewing, 1934) as *Pediculus humanus americanus* Ewing. Their identity and possible relationships to other forms of *Pediculus* were discussed in a subsequent paper (Ewing, 1936) where the existence of two forms of *Pediculus humanus americanus* was reported.

This new species is close to *Pediculus humanus americanus* Ewing in its adult state, but differs from the types of *americanus* in having laterotergites III and IV regularly lobed and in the great length of laterotergite V.

The eggs are very different from those of *americanus*. Most of them possess a low, tubercle-like expansion at the base. But it is in the form of the attachment sheath that the eggs of *pseudohumanus* depart the farthest from those of *humanus*. In the egg of *humanus* (Fig. 1) this sheath is shorter than the egg in length, while in *pseudohumanus* (Fig. 5, *a*) it is much longer. One of the monkeys from which *P.* (*P.*) *pseudohumanus* was taken was a specimen of *Cacajao rubicundus*. In order to find out if a species of *Cacajao* might be infested in nature, skins of two adult individuals of *Cacajao melanocephalus* killed in nature at Rio Maturaca, Brazil, in November, 1930, by E. G. Holt were examined. They showed no evidence of infestation. It should be remembered, however, that negative evidence of this kind based on such a small number of skins means but little. The percentage of individual monkeys of any species that are infested in nature must be very small.

In the adult specimens taken from an Indian woman, laterotergites III and IV are very definitely lobed as in the specimens taken from the

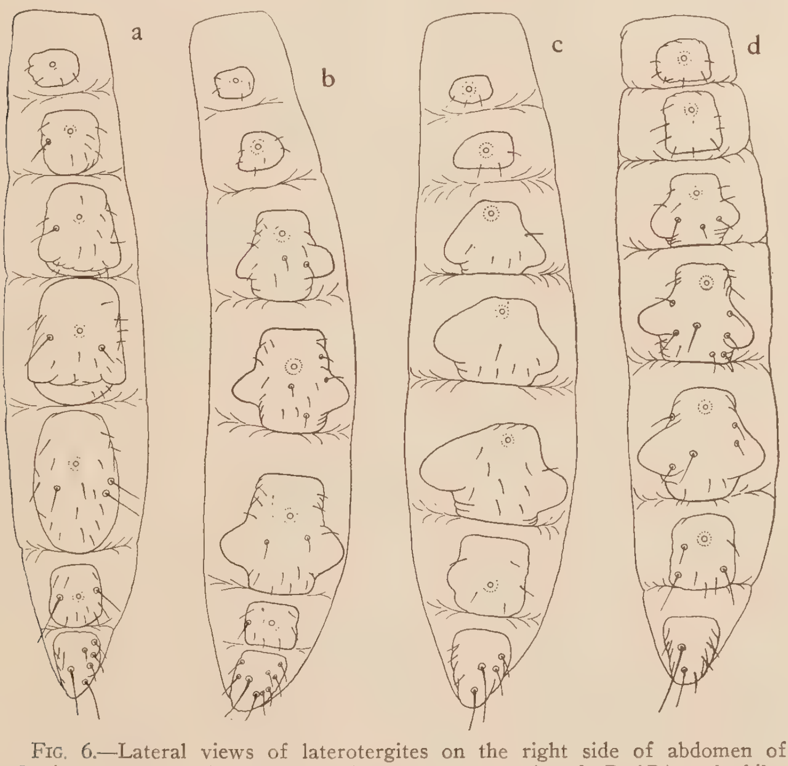

FIG. 6.—Lateral views of laterotergites on the right side of abdomen of *a*, *Pediculus* (*Parapediculus*) *pseudohumanus*, new species; *b*, *P.* (*P.*) *atelophilus* Ewing; *c*, *P.* (*P.*) *chapini* Ewing; *d*, *P.* (*P.*) *lobatus* Fahrenholz. All drawings × 50.

monkeys, while laterotergite V shows a slight tendency toward lobe formation.

Pediculus (*Parapediculus*) *atelophilus* Ewing (1926)

(Fig. 2; Fig. 5, *b*; Fig. 6, *b*)

Female.—Abdomen capable of much distension. Dorsal setae of anterior and posterior transverse rows of a typical abdominal segment very short (easily overlooked), those of middle transverse row short but easily detected. Laterotergites as follows: I subrectangular, slightly broader than long; II similar in shape to I but slightly larger; III about twice as long and broad as II, with well-developed lobes the anterior margins of which do not merge into the anterior margin of laterotergite; IV very similar to III but slightly larger; V similar in shape to III and IV, the largest of all the laterotergites yet occupying only about the posterior three-fifths of the length of the laterotergal area; VI rectangular, in side view appearing as a square. Typical laterotergites each with several inconspicuous setae.

Total length of body of female, 2.985 mm; width, 1.325 mm.

Male.—With the usual differences between male and female and with special differences as follows: Abdomen provided with a few remnants of tergites and sternites, some of the segments having the tergite divided into an anterior and a posterior piece. Laterotergite I reduced to an irregular sclerotized ring and a very small, lateral, detached sclerotized piece; II about the same as in female; V with smaller lobes than in female.

Total length of body of male, 2.230 mm; width, 0.995 mm.

Egg.—Short, stout, considerably swollen on side away from hair, with conspicuous constriction near base, the constricted part being turned toward hair. Nodular area of operculum composed of 8 to 10 peripheral cellulae, 2 to 3 central cellulae, and occupying about one-half of diameter of operculum. Margin of egg shell next to opercular opening turned inward. Wall of cement cup next to hair much thickened toward middle; wall away from hair progressively increasing in thickness from top to base. Attachment sheath rather thick-walled except for lower portion, which varies much in length.

Length of egg, 0.915 mm; greatest width, 0.445 mm. Shortest attachment sheath measured, 0.810 mm; longest, 1.500 mm; average for 6, 1.094 mm.

The egg of this species has been previously described and well figured by Hinman, 1931. The description here given agrees very closely with characters given by this author.

First Nymph.—Dorsal abdominal setae arranged in four longitudinal rows; two rows being paramedian and two dorsolateral. Each paramedian row consisting of seven or eight setae, there being typically one seta in such a row for each abdominal segment. All paramedian setae very minute except the last, which is conspicuous, being about as long as last abdominal segment. Dorsolateral setae less numerous than paramedian; all minute except the last seta, which is about three-fourths as long as last paramedian seta. A lateral row of setae is present, consisting of a single seta to each paratergal area. These lateral setae are larger than the dorsal setae. Laterotergites absent. First two pairs of abdominal stigmata distinctly dorsal in position.

Length of newly hatched first nymph, 0.925 mm; width, 0.380 mm.

This nymph has already been described and figured by Hinman, 1931. Hinman notes its close resemblance to that of the first nymph of *humanus* and states that it is doubtful if the two species can be separated with any degree of certainty in this stage. The chief difference is to be found in the chaetotaxy of the abdomen. In the first nymph of *humanus* there is no striking difference in size between the dorsal abdominal setae of the first seven segments and those of the eighth segment, while in *atelophilus* the setae of the eighth segment are strikingly larger than those of the other segments.

Second Nymph.—In the second nymph the seventh abdominal segment becomes distinctly broader than the others and the laterotergites appear for the first time. Dorsal abdominal setae about twice as numerous as in first nymph and for the first time arranged in definite transverse rows, a single row being present on each abdominal segment. Dorsal setae also arranged more or less in eight longitudinal rows. Lateral setae more numerous than in first nymph and no longer arranged in a longitudinal row on each side of body. Laterotergites very unequal in size; I and II smaller than the others and slightly dorsal in position; III larger than II, quadrangular, without lobes; IV much larger, and more strongly sclerotized than III, also cupped and usually with minute lobes; V much the largest, thickest, most pigmented and most cupped of all the laterotergites and provided with conspicuous lobes; VI similar to IV in size, shape and sclerotization.

Length of second nymph, 1.515 mm; width, 0.675 mm.

Third Nymph.—The third nymph differs from the second in being larger, in having larger and somewhat differently shaped laterotergites and in the chaetotaxy of the abdomen. The dorsal abdominal setae have lost their arrangement in longitudinal rows and are now arranged only in transverse rows, one row to a segment. These rows are incomplete on segments I to VI inclusive, and the setae increase progressively in size from the first to last abdominal segment. Laterotergites I and II much smaller than the others, about equal in size, I being distinctly dorsal and II laterodorsal; III to V heavily sclerotized, strongly cupped and with conspicuous lobes; VI about the size of III but without lobes. No external sexual characters observed in third nymph.

Length of fully engorged third nymph, 1.520 mm; width, 0.905 mm.

Type host.—*Ateles geoffroyi.*

Type locality.—Holotype from skin of type host individual which was kept at the National Zoological Park, Washington, District of Columbia.

Type slide.—U.S.N.M. No. 28105.

Remarks.—Material examined as follows:

From *Ateles geoffroyi:* two eggs from skin (U.S.N.M. 12138) of individual taken in nature, Talamanca, Costa Rica, by W. M. Gabb; many eggs (about rump) from skin (U.S.N.M. 12150) taken in nature, same place, same collector; several eggs from skin (U.S.N.M. 12151) taken in nature, same place, same collector; three eggs from skin (U.S.N.M. 154223) of individual that died in National Zoological Park, May 7, 1909; several eggs from skin (U.S.N.M. 61209) of individual taken in Costa Rica; eggs and male (holotype) from skin (U.S.N.M. 155393) of individual that died at National Zoological Park, September 11, 1909; eggs and first nymphs from skin (U.S.N.M. 154223), without other data; two males and four females collected by E. H. Hinman from young female host brought to this country from the Coto Region, Northern Panama, by E. C. Faust, September, 1930; two males and three females, Ancon, Canal Zone, by L. H. Dunn (received in 1930); one male, nymphs and eggs, from a two-thirds-grown female at the National Zoological Park, October 7, 1933, by H. E. Ewing (female host was one of several individuals taken earlier in the year in the Coto Region of western Panama by C. R. Carpenter and kept in an out-of-doors cage); adults, nymphs and eggs, from a host individual with same data except that lice

were collected October 14; several eggs from live, one-half-grown, dark brown female, November 8 (other data as before); several eggs from two-thirds-grown female, November 28 (other data as before); reared first nymph, from egg taken on large, live, female host, October 31 (other data as before).

From *Ateles pan:* a single female not yet emerged from her nymphal skin, many nymphs and eggs from skin (U.S.N.M. 61284) from Guatemala. (These specimens were wrongly identified by the writer (Ewing, 1926) as *P.* (*P.*) *lobatus* Fahrenholz.)

From *Ateles dariensis:* two males, two females and two nymphs, Ancon, Canal Zone, L. H. Dunn (received in 1930).

From *Ateles hybridus:* a second nymph and eggs from adult female, National Zoological Park, February 15, 1934, by H. E. Ewing.

Among the specimens of the seventeen lots here regarded as *P.* (*P.*) *atelophilus* Ewing there is considerable variation. Some of this is possibly due to hybridization. The species is particularly characterized by the shape of the lobes of the laterotergites and by the fact that the typical laterotergites occupy only from one-half to three-fifths of the length of the laterotergal areas.

Pediculus (*Parapediculus*) *chapini* Ewing (1926)

(Fig. 4, *a*; Fig. 5, *c*; Fig. 6, *c*)

Female.—Body setae very small, most of them minute. Abdomen easily distended by imbibed blood. Laterotergites short, broad, not occupying very much of anterior part of laterotergal areas. Laterotergites as follow: I greatly reduced and varying in shape, considerably broader than long, occupying about one-third length of laterotergal area; II about twice as large as I and with anterior and posterior margins almost straight; III large, three-fourths as long as laterotergal area, with spiracle almost contiguous with anterior margin and with very large lateral lobes, the dorsal one being continuous along its anterior margin with anterior margin of laterotergite; IV very similar to III, but slightly larger; V largest of all laterotergites, but only occupying about three-fourths length of laterotergal area, frequently not so strongly lobed as IV; VI subrectangular, slightly longer than broad, slightly lobed dorsally, and with spiracle situated slightly behind middle of laterotergite. Setae on laterotergites small; largest number on any one laterotergite about ten.

Total length of body of female, 2.800 mm; width, 1.445 mm.

Male.—With the usual differences between male and female and in addition: Provided with a few tergites and sternites which are never large and may be divided so that some of them are represented by two small transverse bars. Laterotergites I and II different from those of female; I a crescent or circle of chitin, partly or completely surrounding first spiracle; II irregularly subrectangular, longer than broad, with spiracle almost contiguous with front margin.

Total length of body of male, 2.250 mm; width, 0.925 mm.

Egg.—Rather slender, side away from hair not swollen, base turned somewhat toward hair. Nodular area of operculum composed of 6 to 9 peripheral cellulae, 1 to 3 central cellulae, and occupying about one-half diameter of operculum. Margin of eggshell next to opercular opening turned inward. Wall of cement cup next to hair very thin at top but considerably thickened toward base;

wall away from hair progressively increasing in thickness from top to base. Attachment sheath with rather thick walls at top, but becoming very thin toward bottom.

Length of egg, 0.825 mm; greatest width, 0.340 mm. Shortest attachment sheath measured, 0.835 mm; longest, 1.470 mm; average for 7, 1.038 mm.

Third Nymph.—Three subequal dorsal setae on each side of abdomen along front margin, indicating fusion of first abdominal segment with second; behind these three setae, on either side, two or three smaller setae indicating presence of fused second abdominal segment. Dorsal abdominal setae increasing in size from second to eighth segment; arranged in incomplete transverse rows on segments I to V, but forming a complete row of eight setae on segments VI to VIII. Laterotergites: I smaller than others, variously shaped, usually more or less oval; II larger than I, subquadrangular, without lobes; III larger than II, sometimes slightly lobed; IV larger than III, cupped, with rather small, but distinct lobes, and occupying about posterior half of laterotergal area; V largest of all laterotergites, strongly cupped, strongly lobed, with spiracle near anterior margin, and occupying about posterior two-thirds of laterotergal area; VI subrectangular, about as large as V.

Total length of body, 1.95 mm; width 0.755 mm.

Type host.—*Ateles ater.*

Type locality.—Type specimens taken from host individual that died at the National Zoological Park, Washington, District of Columbia.

Type slide.—U.S.N.M. No. 28106.

Remarks.—Descriptions based on material as follows: Many males, females and some nymphs in lot material including types taken by E. A. Chapin from host individual, *Ateles ater,* which died at the National Zoological Park in 1921; several eggs from skin of *Ateles ater* (U.S.N.M. 200153), by H. E. Ewing; a few eggs from skin of young male of *Ateles ater,* received from Brazil, which died July 24, 1915.

Material considered as representing stragglers as follows: One male, one female, and one third nymph taken alive from living spider monkey, *Ateles geoffroyi,* at the National Zoological Park, October 23, 1928, by R. W. Wells, H. S. Peters, and H. E. Ewing; adult male, female and several nymphs from *Cebus capucinus imitator,* Ancon, Canal Zone, by L. H. Dunn.

Typical specimens of *Pediculus* (*Parapediculus*) *chapini* are easily distinguished from the other forms occurring on American monkeys by the shortness of the laterotergites, the extreme reduction in size of laterotergite I (particularly in the male), and the reduction in size and number of the abdominal setae. Unfortunately all specimens at hand of this species were taken from captive animals. Since three lots came from the South American spider monkey, *Ateles ater,* it is believed that this species constitutes a natural host for the louse.

Pediculus (*Parapediculus*) *lobatus* Fahrenholz (1916)

(Fig. 4, *b*; Fig. 6, *d*)

Female.—Abdomen may be much distended after feeding. Dorsal setae of anterior and posterior transverse rows of a typical abdominal segment greatly

reduced or absent, but those of middle transverse row present and of moderate length. Laterotergites as follows: I subrectangular, broader than long; II subrectangular, about as broad as I but longer, with spiracle situated in front of middle; III well lobed, considerably larger than II; IV similar to III but larger; V similar to IV, but the largest of all laterotergites; VI without lobes, similar to II except for being more cupped. Each laterotergite has several setae of varying lengths, those on IV and V being more conspicuous.

Total length of body of female, 2.55 mm; width, 1.200 mm.

Male.—Smaller than female and with usual sexual differences found in species of *Pediculus,* with special variations noted as follows: Abdomen provided with a few small tergites and sternites; tergites each typically divided, or almost divided, into two small transverse strips of pigmented chitin. Laterotergite I slightly smaller than in female, varying greatly in shape; II similar to that of female; V apparently less conspicuously lobed than in female.

Total length of body of male, 2.35 mm; width, 0.960 mm.

Egg.—The egg of *P. lobatus* is of the same type as that of *P. atelophilus.* I have failed to find a good character for separating the two.

Third Nymph.—Three subequal dorsal setae present on each side of abdomen along its front margin; behind these setae, on each side, three small setae. Dorsal abdominal setae increasing in size from second to seventh segment; arranged in incomplete transverse rows on segments I to VI, but forming a complete row of ten setae on segments VII and VIII. Laterotergites as follow: I subequal to II, irregularly rounded; II subrectangular; III slightly larger than II, with small lobes; IV much larger than III, conspicuously lobed, strongly cupped, occupying about four-fifths of laterotergal area; V much the largest of all the laterotergites, most strongly lobed, very strongly cupped, occupying about four-fifths of laterotergal area; VI about same size as IV, slightly lobed, strongly cupped, occupying about two-thirds of laterotergal area.

Total length of body, 1.80 mm; width, 0.870 mm.

Type host.—Ateles pan.

Type locality.—(?)

Remarks.—Material examined as follows: Many males, females and eggs and some third nymphs from one (U.S.N.M. 238254) of two infested red-faced spider monkeys, *Ateles paniscus,* which died in 1922, at the National Zoological Park, Washington, District of Columbia. These specimens were collected by the writer at the time of the death of the host. Dr. W. M. Mann obtained these monkeys from some Indians at Beni, Bolivia. The monkeys were pets of the Indians. Just how the Indians came into possession of them is not known, but since they were living within the natural range of the host species, it is highly probable that the monkeys did not come into their hands from exotic sources or through an animal dealer. The lice evidently could not have been stragglers from the Indians themselves.

Specimens regarded as stragglers, examined as follows: Adults, nymphs and eggs from one (U.S.N.M. 238258) of two infested brown-hipped marmosets, *Lentocebus nigricollis,* which died at the National Zoological Park in 1922. These lice were taken by Dr. E. A. Chapin and the writer from the host, a male, that was collected by Dr. W. M. Mann, at Tumu Pasa, Bolivia. The two infested marmosets were brought back from South America in close proximity to the heavily infested red-faced

spider monkeys and evidently obtained their lice from the latter. I have found no evidence indicating that marmosets are infested in nature with any species of sucking lice. It is important to note that the infestation on these marmosets was not heavy.

There is some doubt in regard to the identification of this species with Fahrenholz's *lobatus*. It certainly exhibits strikingly the characters he mentions, yet comes from a different host.

The name *Pediculus lobatus* Fahrenholz was proposed in 1913, but the species was not described until 1916. The type host was given as *Ateles rellerosus*, which is now regarded as Schlegel's spider monkey, *Ateles pan*. In the writer's revision of the American lice of the genus *Pediculus* (1926) he referred to *Pediculus lobatus* a single female that had not yet emerged from her nymphal skin, together with some nymphs and eggs. In this he may have been mistaken.

The *P.* (*P.*) *lobatus* of Fahrenholz has very large laterotergites, the typical ones covering about the posterior three-fourths of the length of the laterotergal area; the lobes are well developed on III and IV but do not extend forward so as to become continuous with the anterior margin of the laterotergites. These characteristics identify Fahrenholz's species with the species which the writer considered as *Pediculus consobrinus* Piaget (Ewing, 1926). If Piaget's *consobrinus* is to be regarded as only *humanus*, as claimed by Ferris (1935), Fahrenholz's name *Pediculus lobatus* apparently should be applied to this Bolivian species. The louse very probably would live on any spider monkey, since it maintained itself for days on a marmoset.

THE POSSIBLE ORIGIN AND PHYLOGENETIC RELATIONSHIPS OF SUCKING LICE OF AMERICAN MONKEYS

The occurrence on American monkeys of lice very closely related to those found on man and the absence of such closely related lice on the apes and monkeys of the Old World presents an interesting problem in evolution. The writer (Ewing, 1924) advanced the suggestion that the pediculid lice of American monkeys were derived from American Indians, when the latter reached the tropical regions of the New World in their southward migrations. If this hypothesis had been the correct one, we should have expected further studies to show (1) new intergrading characters between the lice of man and the lice of American monkeys and (2) a variational change in the members of the genus correlated with geographical distribution.

Has further study produced such evidence? It certainly has. In regard to the first point, a study of the species described in this paper as new under the name of *pseudohumanus* shows that here we have what might rightly be considered a connecting link between the previously

known monkey-infesting species and those infesting man. Further, there is the evidence that this species parasitizes both monkeys and man. In regard to the second point, a comparison of the louse specimens in the large collection of the United States National Museum indicates that the development of the lobes on the laterotergites is directly correlated with the distribution of *Pediculus* species as far as Asia and America are concerned. In some of the man-infesting forms of eastern Asia there is a very slight lobing of the laterotergites; in the lice of prehistoric Indians this lobing is somewhat increased; on *P.* (*P.*) *pseudohumanus* the lobes, though very small, occur on all specimens; finally, in *P.* (*P.*) *chapini,* a Brazilian species on *Ateles ater,* the lobes (Fig. 6, *c*) reach their greatest development.

The writer (Ewing, 1924) also suggested that in the genus *Pediculus* we may have a generalized type that is to an unusual degree free from the influences of its environment. If this hypothesis had been the correct one, we should have expected that further studies possibly would show that the group is (1) a very old one and (2) that it now occurs on widely diversified hosts. In regard to the first point, the antiquity of the genus, the studies here made give but little, if any, evidence. At first thought it appears that the presence of well-developed laterotergites on most of the abdominal segments, and of three transverse rows of dorsal setae on the typical abdominal segments in some of the forms of *Pediculus,* stamps the genus as an old and generalized one. Yet when the lice of the Old World monkeys are examined it is noted that the laterotergites are much reduced in size and number. And as for the presence of three transverse rows of dorsal setae to a typical abdominal segment is concerned, such a condition is not found in any of the other monkey-, or ape-infesting lice, or in the lice of lemurs. However, in the genus *Hoplopleura* and related genera, admittedly very old and generalized forms in many respects, there are three transverse rows of dorsal setae for each typical abdominal segment.

In regard to the second point, the possible occurrence of *Pediculus* on widely diversified hosts, the evidence accumulated so far has been negative. The present writer has examined many live and dead monkeys from the Old and New Worlds and the entire collection of ape, monkey and lemur skins of the United States National Museum without finding any records other than those mentioned in this paper. The presence of *Pediculus* on gibbons has been reported by Fahrenholz (1913, 1916, 1919), and their presence on apes other than the chimpanzee has been surmised. Yet the present writer has examined all of the gibbon skins in the United States National Museum and many from other sources without finding as much as a single nit of any sucking louse. He also has examined several live orangs and many skins of this ape with the

same negative results. The negative evidence, while not in the least conclusive, is entirely against the thesis that *Pediculus* is widely distributed among primate hosts.

In conclusion it can be stated that the evidence brought forth in this paper further supports the writer's previously stated hypothesis that the sucking lice of American monkeys were derived originally from those of American Indians. On the other hand, there is little evidence produced to support the hypothesis that the genus *Pediculus* is a generalized one whose species are to an unusual degree free from the influences of host environment.

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OBSERVATIONS ON THE LIFE CYCLE OF *LOXOGENES ARCANUM* NICKERSON (TREMATODA)*

Wiley W. Crawford

I. INTRODUCTION

With the exception of E. W. Stafford's (1931) report of the presence of the immature stages of *Loxogenes arcanum* in the dragonfly naiads of *Gomphus villosipes* Selys and *Plathemis lydia* Drury, nothing has been reported about the life cycle of this trematode, although the adult was first observed in 1900. Evidently Stafford's identification of the metacercaria of *L. arcanum* was based entirely on structural comparisons with the adult since he did not report any feeding experiments in order to confirm his determinations.

This paper deals with the results thus far secured from a study of the life history of *L. arcanum*. The metacercarial stage has been discovered in nine different species of dragonfly naiads collected from five lakes in the vicinity of Minneapolis and from Little Lake Pelican, near Detroit Lakes, Minnesota. The adult stages have been produced experimentally in two species of frogs, *Rana pipiens* Schreber and *R. clamitans* Latr., the latter constituting a new host record. Notes on the size and incidence of the infection in frogs are also included. While the author feels that he has located the cercarial stage, he is unable to submit adequate experimental proof at this time.

In a short paper published in 1912 Osborn reviewed the literature concerned with *L. arcanum* and also contributed to the general biology of the adult worm. He demonstrated that the genital pore is dorsal instead of ventral, thus correcting an error made originally by Nickerson (1900) and subsequently overlooked by J. Stafford (1905).

Care was exercised in the identification of the dragonfly naiads involved. Representatives of most of the forms concerned successfully metamorphosed in the laboratory, and the identification of the naiad checked against that of the imago.

II. THE KNOWN LIFE HISTORY STAGES

A. The Adult

1. *Description.*—The general morphology of the adult has been ade-

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quately described by Nickerson (1900), J. Stafford (1900, 1905) and Osborn (1912).

2. *Notes on the biology.*—The adults of *L. arcanum* have previously been reported from three localities. Stafford (1900) discovered two specimens encysted in the liver of a bullfrog, *Rana catesbiana,* in Ontario, Canada. Nickerson (1900) in Massachusetts frequently found them in various species of the genus *Rana,* but not in *R. catesbiana,* encysted in the wall of the duodenum at the pylorus. Osborn (1912) reported the finding of adults in three leopard frogs, *Rana pipiens,* collected in the vicinity of St. Paul. In two cases the worms were encysted, one specimen to a cyst, in the wall of the urinary bladder, while in the third one large cyst containing five worms were present on the wall of the duodenum and two smaller cysts, enclosing two individuals each, were lodged in the adjacent ventral mesentery.

During the present investigation the adult trematodes have been found in five leopard frogs, always encysted in the wall of the duodenum immediately posterior to the pylorus. Four of the cases were from a total of 97 large leopard frogs collected from Lake Minnetonka during August and September of 1933. Five specimens were removed from one host; 18 from a second; and 21 from a third. The duodenum, which was heavily infected, and the stomach of the fourth frog were removed and preserved in formalin. In the fifth case, 107 worms were found in one of 16 medium-sized leopard frogs collected at Glenwood Lake July 27, 1933. The wall of the upper part of the duodenum was several times its normal thickness, and as many as 9 worms were removed from a single cyst. The host exhibited normal behavior in spite of this heavy infection.

None of the 114 large and 36 small (metamorphosed the previous summer) leopard frogs examined that were collected from Lake Minnetonka in the spring of 1934 were infected. Sixty-seven small leopard frogs and 31 medium-sized *Rana clamitans,* collected from Lake Johanna on May 16 and 23, 1934, where the incidence of infection of the metacercaria in the dragonfly naiads is known to be high, were examined, but with negative results. Fifteen small leopard frogs were examined at Little Lake Pelican June 2 and 3, 1933, where the heaviest known infection of dragonfly naiads with metacercariae occurs, and no adults were found.

The presence of the parasite only in those frogs collected during the latter part of the summer indicates that the frogs became infected by feeding upon the dragonflies during the latter's transformation during late spring and early summer. The adults of the naiads of *T. spinigera, T. cynosura, G. spicatus* and *L. exusta* which are the most important hosts emerge during the last week in May and in June in the latitude of Minneapolis. The finding of only certain terrestrial insects and other arthropods

in the stomach contents of several of the frogs collected May 23 from Lake Johanna is additional evidence that the frogs do not become infected until the naiads leave the water.

B. *The Metacercaria*

1. *Size and Description.*—The average measurements of four living specimens of the metacercaria of *L. arcanum*, subjected to gentle pressure, are as follows: body 0.43 mm in length, 0.29 mm in width; cuticula 0.004 mm in thickness; oral sucker 0.08 mm in diameter; ventral sucker 0.07 mm in diameter; pharynx 0.04 mm in diameter; excretory bladder 0.16 mm in length, 0.21 mm in width; testes 0.03 mm in diameter. Table 1 gives the individual measurements.

TABLE 1.—*Measurement in millimeters of four living metacercariae of* Loxogenes arcanum

	1	2	3	4
Body length	.38	.45	.50	.41
Body width	.30	.30	.28	.30
Cuticula	.004	.004	.004	.003
Oral sucker	.08	.08	.09	.08
Ventral sucker	.07	.07	.08	.06
Pharynx: diameter	.04	.04	.04	.04
Ex. bladder: length	.16	.17	.15	.16
Ex. bladder: width	.23	.23	.17	.21
Testes: diameter	.02	.05	.04	.03

TABLE 2.—*Measurements in millimeters of five preserved metacercariae of* Loxogenes arcanum. (*Killed under Pressure*)

	1	2	3	4	5
Body length	.68	.65	.57	.32	.59
Body width	.39	.52	.51	.24	.37
Oral sucker	.09	.11	.09	.07	.09
Ventral sucker	.08	.10	.08	.06	.07
Pharynx: diam.	.04	.04	.04	.03	.04
Testes length	.06	.10	.04	.03	.04
Testes width	.06	.10	.06	.03	.04
Ovary: diam.	.03	.05	.03	.03	.03

The average measurements of five permanently mounted specimens killed under gentle pressure in corrosive-acetic fixing fluid and stained in Ehrlich's haematoxylin are as follows: body 0.56 mm in length, 0.41 mm in width; oral sucker 0.09 mm in diameter; ventral sucker 0.08 mm in diameter; pharynx 0.04 mm in diameter; testes 0.05 mm in length, 0.06 mm in width; ovary 0.03 mm in diameter. Table 2 gives the measurements for the individual specimens. Larger specimens were selected for permanent mounts, hence the increase in the average size of the preserved material.

The description of the metacercaria of *L. arcanum* (Fig. 6) is as follows: Body elongate with posterior end prominently truncated when fully extended; more or less heart-shaped when contracted (Figs. 1, 2). Oral sucker subterminal and somewhat larger than ventral; ratio approximately 7:6. Ventral sucker just posterior to middle of the body. Prominent cuticular spines cover entire body surface. Excretory pore prominently indented.

Digestive system not extensive. Prepharynx very short and visible only in living material. Pharynx subspherical and well defined. Esophagus slightly inflated and equal to pharynx in length. Intestinal crura short, curve sharply laterally and end at level of ventral sucker. Usually considerably inflated. Length 0.09–0.11 mm. Width 0.02–0.03 mm. Excretory bladder V-shaped and voluminous, occupying entire posterior half of body. Branches ordinarily terminate opposite ventral sucker. Filled with small round to ovate-shaped granules.

Excretory ducts enter the anterior end of the cornua. At point just anterior to testis each excretory duct forms lateral loop, afer which it divides into anterior and posterior collecting branches. Rudiments of reproductive system well developed and conform very closely to adult relationships. Genital pore dorsal, located between lateral margin and left intestinal crura. Testes compact, round to oval, arranged laterally at ends of intestinal crura. Vasa efferentia extend medially uniting anteriorly and to left of ventral sucker to form vas deferens. Latter proceeds obliquely left joining cirrus sac dorsal to distal end of left intestinal crura. Ovary subspherical, located anterior and to right of ventral sucker. Oviduct curves mesiad toward Mehlis' gland. Uterus extends from medial margin of latter, curves posteriorly dorsal to ventral sucker, turns sharply and proceeds directly to genital pore. Vitellaria not present.

2. *Biology*.—The metacercaria has been found encysted in the following nine different species of dragonfly naiads collected from five lakes in the vicinity of Minneapolis and from Little Lake Pelican, near Detroit Lakes, Minnesota: *Tetragoneuria spinigera, T. cynosura, Epicordulia princeps, Gomphus spicatus, Libellula exusta, L. luctuosa, Erythemis simplicicollis, Celithemis eponina* and *Packydiplax longipennis*. Table 3 gives a summary of the number of naiads examined, number of naiads infected and maximum number of cysts found in a single host for the six lakes where collectings were made.

The evidence thus far accumulated indicates that *T. spinigera, T. cynosura, L. exusta* and *G. spicatus* are the most acceptable hosts. The highest incidence and the heaviest infection were encountered in the *Tetragoneuria* naiads collected from Little Lake Pelican and Lake Johanna. Of the 28 specimens of *T. spinigera* examined from Little Lake Pelican 26 were infected. A total of 636 cysts were found, a mean of 25 per infected host. The largest number obtained from a single naiad was 115; the smallest 4. A total of 330 cysts were found in 17 of the 18 naiads of *T. cynosura* from the same lake, a mean of 19 cysts per infected naiad. The largest number of cysts found in this case was 58; the smallest 3. Of the *Tetragoneuria* naiads collected from Lake Johanna 89 of 102 naiads of *T. spinigera* were infected, while 57 of 74 *T. cynosura* harbored cysts, the mean for the former being 4, the latter 5. The largest number found in a single host was 27 for *T. spinigera*; 30 for *T. cynosura*. Although only a small number of *L. exusta* have been examined thus far, 36 cysts were discovered in a naiad from Lake Johanna and 25 in one collected at Little Lake Pelican. While a fairly high percentage of the naiads of *G. spicatus* examined were infected, the size of the infection was small, the largest number of cysts recorded from a single host being 14. The remaining 5 species were only slightly infected, the largest number of cysts found in any single host being 4.

The metacerceria of *L. arcanum* encysts in subspherical, thin-walled cysts in the abdomen of the dragonfly naiads, either in the fatty tissue or in the muscles of the body wall. Mature cysts are usually from a

yellowish-brown to deep brown in color. Twenty mature cysts (measured in the spring) averaged 0.36 mm in diameter. The smallest was 0.31 mm in diameter; the largest 0.45 mm.

Very small cysts have been recovered from young *Tetragoneuria* and *Gomphus* naiads collected during August and September. Since these naiads develop from eggs that were laid in June, it follows that the dragonfly naiads acquire the infection during late summer while they are still quite small.

Measurements taken in the fall and in the following spring show that the cysts increase in size during the winter months. Ten cysts measured on November 1, 1933, averaged 0.25 mm in diameter, which is approximately 0.10 mm smaller than the average for twenty cysts measured in the spring. Correlated with the enlargement of the cyst is the increase in the size of the metacercaria.

III. EXPERIMENTS TO DETERMINE THE METACERCARIA OF *Loxogenes arcanum*

A. *Source and care of experimental animals.*—The infected dragonfly naiads of *T. spinigera, T. cynosura* and *G. spicatus* which were used in the experiments were collected from Lake Johanna. The frogs used were young *Rana pipiens,* captured in the spring from Bassett Stream, near Minneapolis, where no infections had previously been found and where of the dragonfly naiads that serve as the intermediate hosts only *L. luctuosa* occurs, none of which has ever been found to contain the metacercarial stage. Two young *R. pipiens* raised from tadpoles caught at Lake Johanna were also used. The frogs were kept in large aquaria covered over with wire screen until infected, and were fed on trapped blowflies. Thereafter, they were kept singly in smaller covered aquaria.

B. *Controls.*—Twenty-five of the frogs collected at Bassett Stream and one of the laboratory-raised specimens were examined, and all were found to be negative for trematodes of any sort.

C. *Experimental results.*—A total of 16 frogs were fed cysts identified as those of *L. arcanum* from dragonfly naiads, and in every case young or mature trematodes belonging to this species were recovered later when the treated animal was examined. In all cases the worms were found, either encysted or in the process of becoming so, in the wall of the duodenum immediately posterior to the pylorus. Rather than give the details of the infection of all the experimental animals involved, the results from six, which are representative, will be presented. Frog No. 2 was given 3 cysts from a naiad of *G. spicatus.* Two days later 3 young trematodes were found in the upper portion of the duodenum attached by their suckers to the mucous membrane. No adults were present. Frog No. 3 received approximately 30 cysts from 3 naiads

TABLE 3.—*Showing number of dragonfly naiads examined, number infected and maximum number of cysts present for* Loxogenes arcanum *from six lakes in Minnesota*

	Glenwood Lake			Lake Johanna			Lake Minnetonka			Little Lake Pelican			Crystal Lake			Lake Vadnis		
	No. Exam.	No. Inf.	Max. No.	No. Exam.	No. Inf.	Max. No.	No. Exam.	No. Inf.	Max. No.	No. Exam.	No. Inf.	Max. No.	No. Exam.	No. Inf.	Max. No.	No. Exam.	No. Inf.	Max. No.
T. cynosura ...	19	3	11	74	57	30	34	6	7	18	17	58	3	2	5	7	5	6
T. spinigera ...	21	5	10	102	89	27	36	8	9	28	26	115	5	4	6	6	4	3
L. exusta		no record		13	6	36		no record		3	1	25		no record			no record	
E. princeps	6	0	0	16	2	3	12	1	2		no record		2	1	2		no record	
E. simplicicollis	11	2	3	15	4	3		no record			no record			no record		2	2	2
G. spicatus	8	2	3	40	14	5	1	0	0	12	6	14	23	4	5		no record	
C. eponina		no record		16	3	3		no record			no record			no record			no record	
P. longipennis .	12	2	4		no record			no record		9	3	3		no record			no record	
L. luctuosa ...	15	4	2	22	2	3	6	0	0	1	1	5	5	0	0		no record	

Note:—The figures given here are based on collections made in the fall and spring, 1932–34, in the vicinity of Minneapolis and from June 2–5, 1933, at Little Lake Pelican.

of *T. spinigera.* Seven days later 13 young flukes were recovered, about half of them still free in the duodenum. The other half were partially embedded in the intestinal lining and were removed with dissecting needles. Frog No. 7 was given 40 cysts from 5 naiads of *T. spinigera.* Four weeks later 28 worms were recovered encysted in the wall of the duodenum. About 40 per cent were sexually mature. Frog No. 8 was fed 36 cysts from 4 naiads of *T. spinigera* on April 23, 1934, and 8 cysts from a single naiad of the same species on May 4. May 27, twenty-seven specimens, 22 sexually mature and 5 young, were removed from cysts in the wall of the duodenum. None of the adults had the uterus fully distended with eggs. Frog No. 13 received 31 cysts from two naiads of *T. cynosura.* Eight weeks later 23 sexually mature specimens were recovered from cysts in the wall of the duodenum. In most cases the uterus was well filled with eggs. Frog No. 16, which was raised in the laboratory from a tadpole, received 4 cysts from a naiad of *G. spicatus.* One week later 3 young worms were found in the duodenum. One was partially embedded in the intestinal lining, the others still free living. No adults were present.

The results from the above experiments demonstrate conclusively that dragonfly naiads harbor the metacercarial stage of *L. arcanum,* and that frogs become infected by feeding upon these insects.

IV. EXPERIMENTS THAT ESTABLISH *Rana clamitans* AS A PRIMARY HOST OF *Loxogenes arcanum*

Although Nickerson (1900) reported the finding of the adults of *L. arcanum* in various species of frogs belonging to the genus *Rana,* there is no mention that *Rana clamitans* was one of the hosts involved. The experiments which demonstrate that this frog is a satisfactory host for *L. arcanum* are herein presented.

A. *Source of experimental animals.*—The infected dragonfly naiads, *T. spinigera,* which were employed were collected from Lake Johanna. The frogs used were 12 young specimens of *R. clamitans* secured in February, 1934, from a commercial firm in New Orleans, and cared for in the laboratory until May.

B. *Control animals.*—Eight of the frogs were treated as controls, and when examined proved to be negative for *L. arcanum.*

C. *Outline of experiments.*—Frog No. 1 received 7 cysts from one naiad. Three days later 4 young worms were recovered free in the duodenum. No adults were discovered. Frog No. 2 was fed 20 cysts from 3 naiads. One week later 11 young trematodes were found: 7 free in the duodenum and 4 partially buried in the intestinal wall. No adults were present. Frog No. 3 was given 41 cysts from 5 naiads. Two weeks later 37 young flukes were recovered. All except 6 were encysted.

None of the worms was sexually mature. Frog No. 4 received 25 cysts from 3 naiads. It was being kept for examination four weeks after feeding, but died the third week. Its death was discovered too late to recover the worms.

Thus far, no natural infection of *L. arcanum* has been found in *R. clamitans* by the author, but the experimental results show that this species is an acceptable host.

V. DEVELOPMENT OF *Loxogenes arcanum* IN THE PRIMARY HOST

The growth of *L. arcanum* takes place slowly in the frog, and with such variation among individuals that size is often of little value in determining the age of the developing worm.

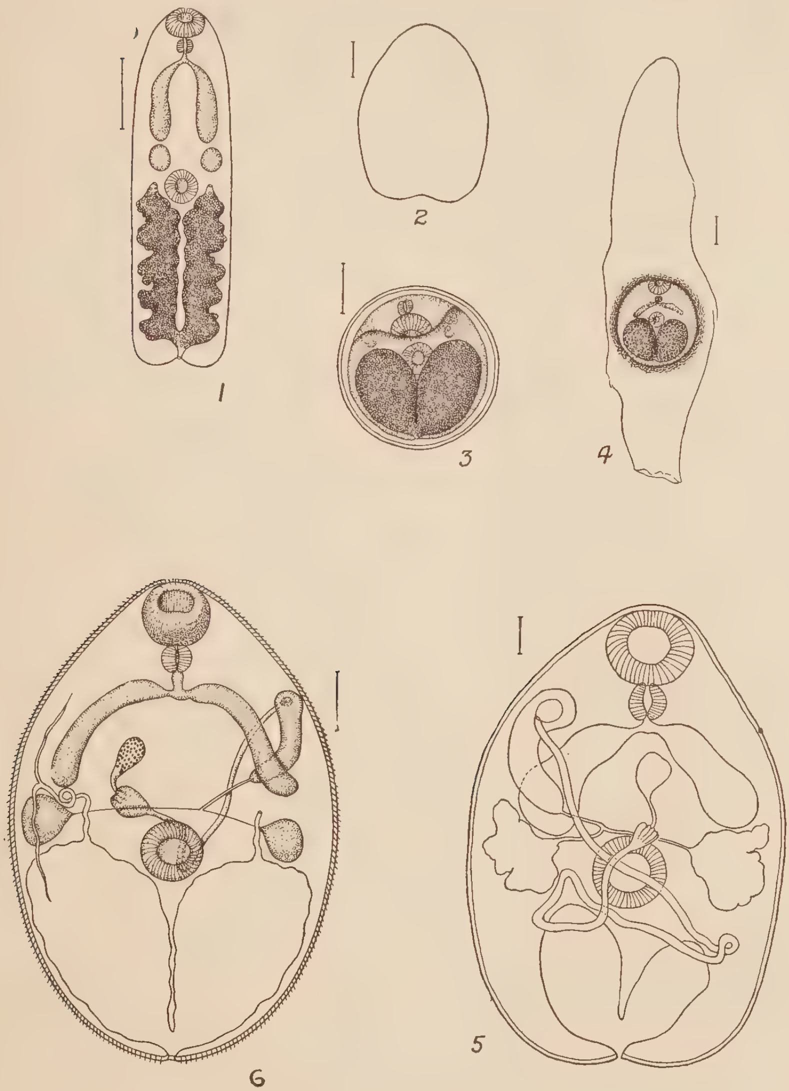
One specimen (Fig. 5), one week old and killed with corrosive-acetic killing fluid, gave the following measurements: body 0.65 mm in length, 0.45 mm in width; oral sucker 0.12 mm in diameter; ventral sucker 0.10 mm in diameter; pharynx 0.05 mm in width; testes 0.11 mm in diameter; ovary 0.05 mm in diameter. This is only a slight increase in size over the metacercarial stage (see Table II). The intestinal caeca were filled with blood, and the uterus had increased considerably in length.

Of 28 specimens removed from a frog four weeks after infection and preserved in 10 per cent formalin, only 12 contained mature eggs in the uterus. The largest representative was 1.44 mm in length, 0.99 mm in width; the smallest 0.81 mm in length, 0.63 mm in width. All of 22 worms five weeks old were found to be sexually mature. Eight individuals killed in corrosive-acetic killing fluid gave the following average measurements: body 1.40 mm in length, 1.01 mm in width; oral sucker 0.20 mm in diameter; ventral sucker 0.16 mm in diameter. The preserved specimens that had remained nine weeks in the frog averaged 1.94 mm in length, 1.52 mm in width, which is approximately the size of those found in the naturally infected frogs (Nickerson, 1900; Osborn, 1912; and this investigation).

The evidence just presented shows that the adults develop rather slowly in the frog, reaching sexual maturity in four to five weeks and full growth in eight or nine. During the first week the young trematodes are free in the duodenum, after which they begin to invade the wall of the organ where they later undergo encystment.

VI. SUMMARY

1. The metacercariae of *Loxogenes arcanum* have been found in nine different species of dragonfly naiads: *Tetragoneuria spinigera, T. cynosura, Gomphus spicatus, Libellula exusta, L. luctuosa, Epicordulia princeps, Erythemis simplicicollis, Packydiplex longipennis* and *Celithemis eponina.*



EXPLANATION OF PLATE

The projected scale represents 0.05 mm for figure 5; 0.075 mm for figure 6; 0.10 mm for the remaining.

FIG. 1. Metacercaria of *Loxogenes arcanum,* ventral view, fully extended. Drawn from a living specimen.

FIG. 2. Metacercaria of *L. arcanum.* Outline drawing of a contracted living specimen.

FIG. 3. Cyst of *L. arcanum.*

FIG. 4. Encysted metacercaria of *L. arcanum* in lobe of fatty tissue.

FIG. 5. Young trematode of *L. arcanum,* dorsal view, seven days old. Drawn from permanently mounted specimen.

FIG. 6. Metacercaria of *L. arcanum,* ventral view. Drawn from permanently mounted specimen.

2. The metacercariae are encysted in the fatty tissue and muscles of the abdominal wall. The largest number of cysts found in a single dragonfly naiad was 115.

3. Notes on the size and incidence of the infection in the intermediate host are given.

4. The metacercariae were verified as those of *L. arcanum* by feeding dragonfly naiads containing the cysts to the leopard frog, *Rana pipiens,* and later finding the immature and mature trematodes in the intestinal tract.

5. Experiments which show that *R. clamitans* is a satisfactory primary host are described.

6. The adults were found to encyst in the wall of the duodenum immediately posterior to the pylorus. During the first week after infection they were free in the duodenum.

7. In the primary host it takes from eight to nine weeks for the worms to reach their maximum size, and about four and one-half weeks to become sexually mature.

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INFECTION OF THE CHICKEN WITH *CAPILLARIA COLUMBAE* (RUD.)*

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There have been several reports of infections of chickens with *Capillaria columbae.* The first record was by Graybill (1924) who also found it in turkeys. Morgan (1932) reported it in England. Reis, Nobrega and Reis (1936) have cited numerous instances of capillaria infection in the domestic fowl.

Pathogenic effects of *C. columbae* in chickens have not been reported. Stubbs and Crawley (1922) described a severe chronic proliferative enteritis in two chickens caused by a mixed infection with *Capillaria* spp. and *Heterakis vesicularis.* A diphtheritic follicular enteritis in one chicken caused by *Capillaria* spp. was described by Graham *et al.* (1929). They found a marked dilation of the intestine anterior to the caeca and a histo-pathological study showed necrosis and sloughing of the epithelium. On the other hand the pathogenicity of *Trichosoma tenuissimum* (Dies.) (= *C. columbae*) for pigeons was reported by Eber (1917) and Schlegel (1918). These workers observed that the infected pigeons showed extreme emaciation and finally died. A severe catarrhal enteritis was found on post-mortem examination.

Graybill (1924) found that the ova of *C. columbae* when incubated in shallow layers of saline solution at 22° to 25° C. were embryonated after 7 days while another culture embryonated in 6 days at 24° to 25° C. He did no feeding experiments. The direct life cycle of *C. retusa* (Cram not Raillet) was experimentally demonstrated by Cram (1932). However, after a restudy of her specimens, Cram (1937) is convinced she was working with *C. columbae* and not *C. retusa.* Cram incubated the ova at 30° C. and found that when they were examined 42 days later they contained fully developed embryos. The embryonated ova were fed to a chicken and a quail and capillaria were recovered from the intestines of these birds 19 and 22 days later, respectively.

A satisfactory vermicide has not been reported for capillaria. Carbon-tetrachloride and tetrachlorethylene have been tried by Cram (1932) and by Rietz (1927) with inconstant results.

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Since *C. columbae* has been found on numerous occasions in the intestines of chickens sent to this laboratory, a study of this parasite was undertaken. The life cycle and its pathogenicity in particular were studied. In addition some experiments were done to test the efficiency of two vermicides against it.

METHODS

The birds used in these experiments were Barred Plymouth Rocks, Rhode Island Reds and Single Comb White Leghorns. These chickens were artificially hatched, brooded, and kept in batteries or individual cages with wire screen floors. Adventitious infection with *C. columbae* was not encountered during the course of this investigation.

To produce heavy infections with *C. columbae* the technique described by Levine (1936*a*) was used. In this method fly larvae consume the putrescible material in feces passed by parasitized chickens. The fecal residue containing the unharmed capillaria ova is moistened and incubated until embryonation takes place. This material is then mixed with the mash and fed to the birds. It was found that when chicken manure was used as a source of infective material coccidia as well as capillaria were being transmitted. Fortunately a number of pigeons which were being kept at the laboratory were found to be naturally infected with *C. columbae*. Consequently pigeon manure was used as a source of infective material. In spite of the fact that the pigeons were passing coccidial oöcysts transmission of coccidiosis to the chickens did not result. This corroborates the results of Nieschulz (1925), cited by Becker (1934), who was able, with pigeon coccidia, to produce only a mild and transient infection in 2 out of 23 chickens.

Worm counts were done by scraping the mucosa of the entire intestine into a dish of warm water and examining it in small portions under a wide field binocular microscope. The procedure was facilitated by adding to each portion a few drops of 20% NaOH solution to dissolve the mucus.

Statistical analyses of the weight records were done according to the method of Fisher (1934) for paired data. The probability table used in determining the significance of mean differences was Student's table for 't' as modified by Livermore (1934). Mean differences were considered significant if the odds were 19:1 or greater.

EXPERIMENTAL

Life Cycle Studies

Ova of *C. columbae* procured from female worms which had been removed from the intestines of chickens, were placed in shallow layers of distilled water and incubated at 30° C. Embryonation was completed

on the 6th or 7th day, at which time microscopic examination revealed the fully formed coiled and moving embryo within the egg-shell. The embryonation time agrees with Graybill's results (1924) although he incubated the ova at lower temperatures. Suspensions of the embryonated ova were pipetted directly into the crop of a large number of parasite-free chickens ranging in age from 28 to 66 days. Periodic examinations of the feces from these birds were done. Fertile non-embryonated ova did not appear in the feces until 21 days after the infective feeding. The birds were autopsied from 36 to 294 days after feeding the embryonated ova. In every case mature specimens of *C. columbae* were found in the intestinal mucosa.

In one experiment 8 birds, after being starved for 24 hours, were fed embryonated ova mixed with the feed. One bird was autopsied on each of the following 6 days and on the 10th and 13th day after the infective feeding, respectively. Microscopic examination of fresh scrapings from the mucosa of the small intestine showed active larvae 24 hours after the infective feeding. That these larvae had already started to penetrate the intestinal epithelium was demonstrated in stained tissue sections of the intestine. As the parasites got older they increased in size and were found partially imbedded directly beneath the epithelium of the villi. Occasionally some worms were found deep in the mucosa beneath the epithelium of the intestinal glands but generally the villi harbored most of the worms. Although in heavy infections *C. columbae* were found in all portions of the intestine including the duodenum and caeca, generally the parasites were most commonly encountered in the mucosa of the lower two-thirds of the small intestine.

Pathogenicity of C. columbae *for Chickens*

Twenty-six Rhode Island Red chickens, 8 weeks old, were divided into two groups so that each bird in one group was matched with a bird of the same sex and weight in the second group. This was done to insure a similar distribution in both groups thereby facilitating the statistical analysis of the weight records which were made at regular intervals. Each group was kept in a separate compartment of a holding battery with wire screen floors. Feed and water were before the birds at all times. Infection in group 1 was effected by mixing with the mash pigeon manure which contained embryonated *C. columbae* ova prepared as already described. The birds ate the contaminated feed readily and generally consumed all of it within two hours. Regular feed was then placed before them as usual. Infective material was fed on September 15, 16, 17, 19, 24, 29, October 5 and 9. No attempt was made to count the number of ova fed.

Clinical Symptoms: The first symptoms were noted 12 days after the first infective feeding. In the feces of the infected group were found

numerous pinkish colored shreds of material which had a soft, moist, somewhat rubbery texture. Microscopic examination of wet preparations of this material showed it to be composed of strings of mucus, necrosed epithelial cells and numerous erythrocytes, granulocytes and lymphocytes. In one instance there was observed a long strip of epithelial cells still joined together and retaining the shape of a villus. Entwined in this material were large numbers of active immature *C. columbae* apparently of different ages since there were marked differences in the sizes of these worms. During the next four days the elimination of epithelium and inflammatory exudate was greatly increased which caused the feces to become quite fluid. The infected birds exhibited a depressed attitude and stood huddled together with wings and tails drooping and feathers ruffled. During the following two weeks the character of the feces gradually returned to normal and the majority of the infected chickens regained their normal appearance. Four of the birds, however, lost weight steadily, became extremely emaciated and weakened, and either died or were destroyed 24, 25, 41 and 44 days, respectively, after the first infective feeding. Nervous symptoms were not noticed in the parasitized birds.

Examination of the weight records in Table 1 shows that during the period up to and including the ninth day after the first infective feeding there were no significant differences between the mean weights of the control and the infected birds. On the 15th day after the first infective feeding the mean weight of the infected group was .31 pounds less than that of the controls. It should be noted that this weight loss occurred at about the time that the first clinical symptoms were observed. When this weight difference was analyzed statistically it was found to be highly significant, for each parasitized bird had lost weight during that week while the controls had made normal gains. During the following three weeks the weight differences were substantial and significant statistically. Although the mean weight difference between the control and the infected groups at the end of the last week of the experiment was the largest recorded, that difference was found to be not significant. The weights of two emaciated birds in the parasitized group served to lower the mean weight substantially but the other birds in that group had made substantial gains and weighed about the same as the controls. In other words, the general trend in the parasitized group was towards recovery.

Four days after the last weight records were taken all the birds were autopsied and the worms counted. In no case did the number of parasites found in any single bird exceed 14. On the other hand, the worm counts of the birds that had died or that were destroyed as a result of the infection ranged from 1555 to 4734. The very great disparity between the number of parasites in the dead or dying birds and in the sur-

vivors, coupled with the observation that large numbers of parasites were being eliminated in the feces during the acute stage of the infection, suggests that "self cure" must be credited with a rôle in the survival from this infection. Undoubtedly the resistance of each individual bird largely determines to what degree this "self cure" can operate.

TABLE 1.—*Effect of infection with* Capillaria columbae *on weight (in pounds) of eight-week-old chickens. Infective material fed Sept. 15, 16, 17, 19, 24, 29, Oct. 5 and 9.*

Date	Sept. 1	17	24	30	Oct. 6	12	19	26
Days after first infection	–14	2	9	15	21	27	34	41
Mean weight infected birds Group 1	1.1	1.9	2.2	2.0	2.2	2.2*	2.5*	2.7*
Mean weight control birds Group 2	1.1	1.9	2.2	2.3	2.6	2.6*	2.9*	3.2*
Mean difference ± standard error	0	0	0	.3 ± .05	.4 ± .08	.4 ± .10	.4 ± .13	.5 ± .23
Significance of mean differences	–	–	–	+	+	+	+	–

* 11 birds only; all other mean weights of infected and controls, are on 13 birds.

Lesions: Birds infected with a few worms showed no changes in the intestine. Heavy infections caused a moderate thickening of the intestinal mucosa with reddened areas varying from pinhead hemorrhagic spots to diffuse hyperemia of large portions of the mucosa. In some instances very little or no exudate was present while in others the mucosa was covered with large amounts of catarrhal exudate ranging in color from opaque white to a translucent salmon pink. In one trial several of the birds showed a severe necrotic enteritis. Examination of the necrosed epithelium disclosed not only enormous numbers of immature capillaria but also a few coccidia. Since heavy infections with *C. columbae* alone never produced such lesions, the coccidia together with the capillaria were undoubtedly responsible for the extensive necrosis. On a number of other occasions the intestines of parasitized birds showed no abnormal changes in spite of the fact that the number of worms ranged from 1500 to 5000. This lack of gross inflammation in spite of a heavy infection may be so misleading that one may easily overlook the presence of these parasites.

The microscopic changes, for the most part, corroborated the gross findings. There was a dilation of the capillaries in the villi with an increased mucus production by the goblet cells in some cases. The parasites were found beneath the epithelium of the villi and in some instances the villi were pierced from one side to the other. In a few cases the parasites were found to have penetrated to the muscularis mucosa.

Where the parasites were cut longitudinally, it was found that the epithelium immediately above the worm either was in the process of

being shed or was completely detached from the villus. In most cases although the epithelium above the worm was still continuous the cells themselves were necrosed, atrophic and formed a very thin membrane. These findings explain the presence of epithelial cells in the discharges of parasitized birds. Aside from capillary congestion there was little local reaction around the worms themselves. This corroborates our findings in those cases where extremely heavy parasitisms were encountered in apparently normal intestines. There can be no doubt that the damage done by *C. columbae* results in part from the desquamation of the intestinal epithelium. This may be due either to the mechanical action of the worms or to the action of enzymes produced by the parasites in their migration through the tissues, or to both. Where large areas of mucosa have been denuded of epithelium, secondary bacterial infection could very easily gain headway and produce a necrotic enteritis.

THE EFFICIENCY OF TOBACCO DUST FOR THE PREVENTION OF INFECTION

The feeding of tobacco dust in the mash from the day of hatching has been shown to be ineffective for the prevention of infection with *Ascaridia lineata* in chickens (Levine 1936*b*). Similar experiments were done to test the efficiency of tobacco dust for the prevention of *C. columbae* infection. Fifteen Rhode Island Red chickens, 3 months old, were fed a mash containing 2% tobacco dust (nicotine content 1.75%) by weight. This mash was kept constantly before the birds throughout the duration of the experiment. Two days after being started on this mash 607 grams of pigeon manure containing embryonated *C. columbae* ova were fed to the entire group over a period of ten days. Postmortem examination of the birds at various times after the infective feedings had terminated showed that the parasites not only invaded the intestinal epithelium but that they grew to maturity. That absolute prevention of the parasitism was unsuccessful cannot be doubted. However, since quantitative studies including a control group were not done, it cannot be stated with certainty whether or not some degree of protection was conferred.

TREATMENT WITH CARBON-TETRACHLORIDE AND TETRACHLORETHYLENE

Another series of experiments were done with individual birds infected with *C. columbae*. These birds were placed in separate cages, starved for 12 to 18 hours after which the anthelmintic was introduced directly into the crop. Feed was placed before the birds 1 to 3 hours after the drug was administered. All the manure passed for 48 hours following the treatment was collected in pans holding enough 1% formalin solution to cover it. At the end of this time the birds were destroyed and counts were made of the worms in the intestines and in the

manure. The efficiency of the drug was then calculated in the usual manner.

Five birds (average weight 2.5 pounds) were dosed with 1, 2, 3, 4, and 5 cc carbon-tetrachloride, respectively. This experiment was twice repeated. The results were quite erratic. The efficiency ranged from 0% (7 birds) to 39% (1 bird). There was no correlation between the efficiency of the drug and the amount administered.

In another experiment each of two birds was dosed with 2 and 3 cc tetrachlorethylene, respectively. This experiment was also twice repeated. The efficiency in 5 birds was 0% and in one was 2%.

Apparently neither of the drugs used was effective in removing the parasites.

DISCUSSION

The loss of weight, extreme emaciation and death of chickens heavily parasitized experimentally with *C. columbae* as recorded in this paper confirms the reports by various workers on the pathogenicity of capillaria for chickens. The gross lesions in the pure infections resembled those described by Eber (1917) and Schlegel (1918) in pigeons.[1] Desquamation of the intestinal epithelium in cases of *C. columbae* infection apparently is similar to that of the esophageal and crop epithelium in pheasants parasitized with *C. annulata,* described by Graham (1935). The fact that this desquamation and catarrhal enteritis are the factors responsible for the elimination of a tremendous number of parasites is another example of the protective action of an inflammatory reaction. This "self cure" is quite marked under experimental conditions when heavy infecting doses are fed over a short period of time and when reinfection is prevented. Whether or not natural exposures with continual reinfection over a long period of time would elicit the same response on the part of the host cannot be answered at this time. Proliferative necrotic enteritis as described by Stubbs and Crawley (1922) and Graham *et al.* (1929) was not produced in our experimental birds except in a few cases where coccidiosis was a complicating factor.

The fact that pigeons may readily transmit the infection to chickens has not been taken into account by other workers in discussing the prevention and control of this parasitism. A small number of parasitized pigeons with easy access to any portions of chicken yards or ranges may easily be a constant source of infection for a flock of chickens. An obvious control measure, therefore, would be to confine all barnyard pigeons on poultry farms.

[1] Wehr (1937, J. Parasitol. 23: 573) in a recent abstract report on *C. columbae* in pigeons confirms these observations, as well as several points on the life history recorded in the present article.

Our results of the treatment of *C. columbae* infection with carbon-tetrachloride and tetrachlorethylene are at variance with those of Rietz (1927). It is possible that had the medication been repeated as Rietz had done, an increase in efficiency might have resulted.

SUMMARY

The direct life cycle of *Capillaria columbae* (Rud.) was confirmed. Complete embryonation of the ova takes place in shallow layers of distilled water at 30° C. within 6 to 7 days. Twenty-four hours after the ingestion of the ova by chickens, the larvae can be found penetrating the intestinal mucosa. The worms mature in 21 days at which time fertile non-embryonated ova are found in the feces of the parasitized birds.

A severe infection with *C. columbae* was experimentally produced in chickens. The clinical symptoms and weight records of the parasitized birds showed that this parasite was pathogenic for fowls and heavy infections caused loss of weight, emaciation, and death. The lesions consisted of a catarrhal enteritis with desquamation of the intestinal epithelium.

The comparative ease with which parasitized pigeons may transmit *C. columbae* to chickens suggests the necessity for the elimination of pigeons in any control program.

The attempt to prevent infection by feeding mash, in which was mixed 2% tobacco dust by weight, was unsuccessful. Individual treatment of birds with single doses of carbon-tetrachloride and tetrachlorethylene likewise was not successful.

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HAEMOPROTEUS SP. FROM THE COMMON BLACK DUCK, *ANAS RUBRIPES TRISTIS**

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The genus *Haemoproteus* has been described from a wide variety of birds. However, it has been recorded from only six species of ducks, and none of these reports were from the North American continent. In view of the current low level in our duck population in North America, studies on the diseases of these birds, particularly those likely to be contracted by the fledgelings, are very urgently needed.

The common black duck, *Anas rubripes tristis,* is one of the very few species of ducks that nests in the eastern part of the United States. During the latter part of the summer of 1936 at the Austin Ornithological Research Station, located on Cape Cod, Massachusetts, the blood of 85 of these ducks was examined for parasites. Six of these birds (8%) were found to harbor low grade infections of *Haemoproteus*. The author also examined slides from this same species of duck made at the Austin Station by Dr. Willard C. Greene of Boston, during February, 1933, in which low grade infections of the same parasite were seen. This demonstrates the fact that the infection is carried over the winter in the blood stream of some of the infected birds to be a potential source of spread of the organisms during the following nesting season.

Johnston and Cleland (1909) found one duck (*Nettion castaneum* Eyton) out of two examined, in Australia, to be infected with *Haemoproteus*. On the basis of gametocyte morphology and new host-record they named their form *Haemoproteus nettionis*. The following year Cleland and Johnston (1910) referred to this same parasite as *H. nettii* and to the host as *Nettium castaneum* Eyton. Plimmer (1912, 1915) allocated to the species *H. danilewskyi*—a general name used at that time for all haemoproteids—parasites he observed in the blood of three species of ducks (*Aythya baeri, Nettopus coromandelianus* and *Casarca tadornoides*) examined at autopsy at the London Zoological Gardens in England. Rodhain, *et al.* (1913) reported *Haemoproteus* from a wattle duck (*Sarcidiornis melanota*) in the Belgian Congo. Leger (1918) described *Haemoproteus* which he found to be common (33 out of 65 examined) in a domesticated duck (*Anas moschata*) in French Guiana. Schwetz (1931) reported *Haemoproteus* from the Belgian Congo where

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he found it to be present in the peripheral blood of 3 of 14 wild ducks (*Anas* sp.) examined.

The distinguishing characteristics of the previously reported forms as compared with the present *Haemoproteus* are summarized in the accompanying table. The gametocytes observed in the common black duck

TABLE 1.—*Distinguishing characteristics of the gametocytes of the haemoproteids reported from ducks*

Host*	*Nettion castaneum*	*Sarcidiornis melanota*	*Cairina moschata*	*Anas rubripes tristis*
Parasite	*Haemoproteus nettionis*	*H.* sp.	*H.* sp.	*H.* sp.
Authority	Johnston & Cleland 1909 (1910)	Rodhain, *et al.* 1913	Leger 1918	Herman 1938
Size of parasite	$18 \times 4\ \mu$ (Immature ♂ form)			♂ = $20.5 \times 3.5\ \mu$ ♀ = $20.5 \times 2.7\ \mu$
Granules	Large; 13 in one ♂ 24 and 30 in 2 ♀♀ larger size in ♂♂	Granules are present	4–5 large irregular or rod-shaped surrounded by fine dust-like pigment	Range: 0–13, usually 4–6; round or rod-shaped; black; usually polar
Nucleus of parasite			Central	In ♀ irregular in shape and usually central; in ♂ diffuse, more concentrated in center
Nucleus of host-cell	Displaced	Displaced	Not displaced	Usually displaced, more evident in ♂♂

* Plimmer (1912, 1915) has reported, as *H. danilewsky* Kruse, 1890, forms observed in three species of ducks at the London Zoological Gardens. Since he gives no data on the morphology of these forms as they appear in the duck's blood, they have not been included in this table. Schwetz (1931) reported *Haemoproteus* from *Anas* sp. from the Belgian Congo but gave no description.

have no effect on the size of the host-cell that could be determined by comparative measurements of 50 infected blood cells as compared with the size of 50 uninfected erythrocytes. The parasites usually displace the host-cell nucleus. The figures for the size of the gametocytes given in the table are median values of measurements made on 25 macro- and 25 microgametocytes.

The female forms (Fig. 1, a) have a cytoplasm with an alveolar structure. The cytoplasm stains blue with Giemsa; the nucleus is colored red. The median size of the macrogametocyte based on 25 measured forms is $20.5 \times 2.7\ \mu$, ranging from $13–28\ \mu \times 2–3.5\ \mu$. The nucleus is irregularly rectangular with a median size of $3 \times 2\ \mu$, the range being $2.5–5\ \mu \times 1–3\ \mu$. It is usually in the center of the parasite. Generally from 4 to 6 black pigment granules are present but some forms contain no pigment while as many as 13 grains have been observed. The granules are usually round but frequently appear rod-shaped. The organism almost always fills the entire space between the host-cell nucleus and the periphery on one side of the red blood cell. The nucleus is usually dis-

placed. Macrogametocytes (gametes?) have also been observed free in the blood plasma (Fig. 1, b).

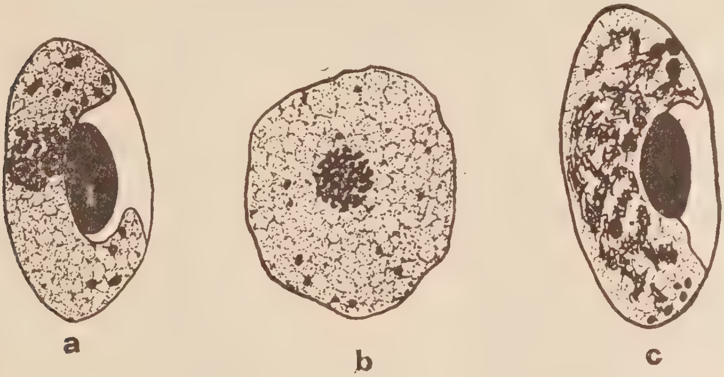

FIG. 1. *Haemoproteus* sp. from the common black duck, *Anas rubripes tristis:* (a) macrogametocyte in red blood cell (13 grains of pigment with polar distribution), (b) macrogametocyte free in blood plasma (scattered pigment granules), (c) microgametocyte in red blood cell (pigment present as 5 course grains and 5 finer granules). Magnification about 3000 ×.

The cytoplasm of the microgametocyte (Fig. 1, c) stains a very pale pink. The red-stained nucleus, though mostly concentrated in the central portion of the parasite, tends to diffuse throughout the organism. The median size of the microgametocytes in 25 measured specimens is 20.5×3.5 μ, ranging from $14–28$ μ $\times 2–5$ μ. As in the female forms, the organism occupies all the space between the nucleus and the periphery on one side of the host-cell, tending to displace the nucleus to a greater extent than does the macrogametocyte. The microgametocytes observed were much broader than the macrogametocytes and it appears that this fact could account for the apparent greater displacement of the host-cell nucleus in these forms. The pigment of the male forms is distributed as in the female gametocytes.

Nothing is known of the life-cycle of the haemoproteids of ducks. It is impossible to distinguish many of the species of *Haemoproteus* which have been described from birds only on the basis of gametocyte morphology and host records above. Therefore, since only gametocytes have thus far been observed in the ducks, no attempt is made to designate the present form either as a species already reported or as a new one.

SUMMARY

Haemoproteus is described from 6 common black ducks (*Anas rubripes tristis*) out of 85 examined at the Austin Ornithological Research Station, Cape Cod, Massachusetts, during the summer of 1936. This is believed to be the first report of this genus from a North American duck.

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SOME CESTODES OF FISH FROM TORTUGAS, FLORIDA*

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The cestodes in the present collection were collected at the Biological Laboratory of the Carnegie Institution of Washington at Dry Tortugas, Florida, in 1930–1932 by Dr. H. W. Manter, under whose direction this study was made. Of the sixteen species reported, fourteen have been previously described, and two species seem to be new. Thirty species of cestodes of fish have been previously reported from Tortugas (Linton, 1909, and Potter, 1937). In this paper are given six new locality records and eleven new host records, as well as descriptions of two new species. New locality records are indicated by ♯; new host records by *.

ORDER PSEUDOPHYLLIDEA Carus, 1863

Family Ptychobothriidae Lühe, 1902

Genus *Clestobothrium* Lühe, 1899

1. *C. crassiceps* (Rud., 1819) Lühe, 1899♯.

Several specimens in each of two specimens of *Merluccius bilinearis* (Mitchill), in a single specimen of *Chlorophthalmus truculentus* Goode and Bean,* and in three specimens of *Merluccius* sp. All of these hosts taken at depths of from 200 to 390 fathoms.

Genus *Ptychobothrium* Lönnberg, 1899

2. *P. belones* (Duj., 1845) Lönnb., 1869♯*.

Syn: *Dibothrium restiforme* Linton, 1891.

Two specimens from *Strongylura notata* (Poey) and one specimen from *Tylosurus raphidoma* (Ranzani). This species has been recorded from *Tylosurus caribbaeus* (LeSueur), from Woods Hole, Mass.

ORDER TETRAPHYLLIDEA Carus, 1863

Family Onchobothriidae Braun, 1900

Genus *Platybothrium* Linton, 1890

3. *P. hypoprioni* Potter, 1937.

One specimen from *Scoliodon terrae-novae* (Richardson)* and many specimens from *Hypoprion brevirostris* Poey. This cestode was originally described from this collection, but *S. terrae-novae* is here recorded as a new host.

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Genus *Phoreiobothrium* Linton, 1889

Linton, in 1889, erected a new genus, *Phoreiobothrium*, for a new cestode, *P. lasium*, and assumed that the bothridia were tubular. Southwell (1925), acting upon this assumption, placed *Phoreiobothrium* in synonymy with *Cylindrophorus* Diesing, 1863. Diesing's genus was based on a set of figures by Wagener in 1854, who gave no description to accompany the figures. Later work has shown that Wagener probably figured three different species of cestodes, one of them a species of *Platybothrium*. Perrenoud (1931) made sections of the scolex of *Phoreiobothrium triloculatum* Linton, 1901, which proved indisputably that the bothridia were not tubular or hollow. Until the study of authentic material shows otherwise, Diesing's *Cylindrophorus* should be allowed to stand, or be considered as a *nomen nudum*. For the above reasons the genus *Phoreiobothrium* is recognized in this paper.

4. *P. lasium* Linton, 1899*.

Numerous specimens from *H. brevirostris* on two occasions. The bothridia in these specimens are not tubular, and there is some possibility that this material represents a new species. The posterior loculi were quite invisible in most specimens; a variable number were faintly discernible in a few specimens.

Genus *Pedibothrium* Linton, 1909

5. *P. longispine* Linton, 1909.
6. *P. brevispine* Linton, 1909.

Several specimens of each in *Ginglymostoma cirratum* (Bonnaterre).

Family Phyllobothriidae Braun, 1900

Genus *Anthobothrium* van Ben., 1850

7. *A. laciniatum* Linton, 1890*.

Several specimens from *H. brevirostris*.

Genus *Phyllobothrium* van Ben., 1849

8. *P. lactuca* van Ben., 1850‡*.

Many specimens from *H. brevirostris*. Although much smaller than previously described specimens, there seem to be no other differences which might be specific.

9. *P. dasybati* Yamaguti, 1934‡*.

Numerous specimens from *H. brevirostris*. These specimens, especially the strobila, are smaller than that of the original description, and the cirrus sac is globose, rather than oval. In both cases, however, the genital atria are unilateral in position.

Species of *Phyllobothrium* are difficult to differentiate. If more reliable criteria were known, these two forms from so widely different localities and hosts might be recognized as different species.

10. *P. tumidium* Linton, 1922‡*.
Two specimens from *Scoliodon terrae-novae.*

ORDER TRYPANORHYNCHA Diesing, 1863

Family Tetrarhynchidae Cobbold, 1864

Genus *Otobothrium* Linton, 1890

11. *O. penetrans* Linton, 1907*.
One specimen from *S. terrae-novae* and eight specimens from *Carcharias limbatus* Müller and Henle.

Genus *Tentacularia* Bosc, 1797

12. *T. insignis* (Linton, 1924) n. comb.‡*
Syn: *Rhynchobothrium insigne* Linton, 1924.
Seven specimens from *H. brevirostris.*
13. *T. lineata* (Linton, 1909) n. comb.
Syn: *Rhynchobothrium lineatum* Linton, 1909.
Numerous specimens from *Ginglymostoma cirratum.*
14. *T. similis* (Linton, 1909) n. comb.
Syn: *Rhynchobothrium simile* Linton, 1909.
Numerous specimens from *G. cirratum.*

15. *Tentacularia perelica* n. sp.

(Figs. 1 to 7)

Specific diagnosis: With the characters of the genus. Small, slender forms, up to 33 mm long. Scolex (fig. 1) 2.3 mm long. Bothridia 0.49 mm long by 0.41 mm wide. Pars vaginalis 1.04 mm long. Pars bulbosa 0.48 mm long by 0.50 mm wide. Bothridia two, heart-shaped, emarginate posteriorly, dorsal and ventral in position. At middle of scolex each proboscis sheath runs straight for about 0.11 mm, parallel to the long axis of the scolex, then continues anteriorly in loose spirals (fig. 6). At the "brackets" thus formed, the direction of spiraling is reversed. Bulbs comparatively short, averaging 0.16 mm wide; wider and slightly separated from each other at posterior ends. Hooks (figs. 2, 3, 4, and 5) dissimilar, from 4 to 37 μ long. At outer side of base of each proboscis is a closely-packed group of very small flattened, triangular scales with slightly recurved tips. These continue anteriorly in five single rows along outer edge of proboscis. On opposite side from scales is a double row of large rose-thorn shaped hooks, 16 by 14 μ. Other hooks long, slender, with recurved tips, of different lengths, the longest 37 μ. Hooks arranged in spirals, with a group of four to five small hooks between each distinct spiral on outer edge of proboscis. Proboscides average 0.06 mm in diameter. Strobila acraspedote, euapolitic, thin. Sex organs (fig. 7) characteristic for the genus. Testes about 130 per proglottid, 0.06 mm in diameter; cirrus globose, without spines. Ovary bilobed, each lobe about 0.20 mm in diameter. Vitelline glands in two lateral rows, interrupted on poral side in region of cirrus sac. Genital atrium in posterior part of middle third of proglottid. Eggs not seen.

Host: Hypoprion brevirostris.
Location: Spiral valve.
Localiy: Dry Tortugas, Florida.
Type: U.S.N.M. No. 9064 (Paratype: No. 9065).

Discussion: No literature was found which refers to any brackets such as those described for this species. Some authors do not figure the proboscis sheaths at all, which presumably means that these structures have no unusual features. Both the brackets and the reversal in direction of coiling of the sheaths seem to be distinctly characteristic for this species and for the species described below. The hooks of *Tentacularia perelica* resemble most closely those of *T. elongatus* (Rud., 1809) as described by Linton (1899). *T. elongatus* was described under the generic name *Tetrarhynchus,* but the nature of the bothridia place it in *Tentacularia. T. elongatus* has a similar group of closely-packed scales at the base of the proboscis, and also has a variety of shapes and sizes of hooks on the distal portion. There are differences in the size and shape of the larger hooks, and there are no definite rows of scales running the length of the proboscis as in *T. perelica.*

T. perelica is also related to *T. lepida* Chandler, 1935; *T. spiracornutum* (Linton, 1907); and a form described as *Rhynchobothrium* sp. by Linton (1909). None of the three above named species has the characteristic group of scales at the base of the proboscis, and there are specific differences in the sizes and shapes of the hooks.

The name *perelica* is from *peri:* around; and *helix:* spiral, and refers to the reversal in spiraling of the proboscis sheaths.

16. *Tentacularia pseudodera* n. sp.

(Figs. 8 to 12)

Specific diagnosis: Small forms, up to 42.0 mm long. Scolex (Fig. 12) 3.11 mm long. Bothridia 0.58 mm long by 0.61 mm wide. Pars vaginalis 1.59 mm long by 0.78 mm wide. Pars bulbosa 0.91 mm long by 0.75 mm wide. Bothridia two, rounded, with slight median posterior indentation; dorsal and ventral in position. At middle of scolex proboscis sheaths run straight for from 0.11 to 0.17 mm, parallel to the long axis of the scolex, then continue anteriorly in loose spirals. At the "brackets" thus formed the direction of spiraling is reversed. Bulbs close together, slender, 0.91 mm by 0.19 mm. Head and neck not clearly separated, the bulbs appearing to extend a short distance into the neck, due to a constriction opposite the posterior end of the bulbs. Hooks (figs. 9, 10, and 11) dissimilar, from 11 to 19 μ long. On inner side of proboscis are three longitudinal rows of small hooks (11 μ) running the entire length of the proboscis. Other hooks of three types: large rose-thorn type; long pointed hooks with simple bases, shaped like an attenuated letter S; and heavy hooks with well developed roots and long, heavy blades. Hooks arranged in spirals interrupted only by the middle row of the three longitudinal rows of hooks. Strobila acraspedote, thin. Sex organs characteristic for the genus. Testes small, about 0.03 mm in diameter; cirrus sac pyriform, 0.16 mm wide by 0.17 mm long. Ovary very small, about 0.15 mm in diameter; about 1/3 of entire length of proglottid from posterior end. Vitelline glands in two lateral rows, interrupted on poral side in region of cirrus sac. Genital pore lateral, near middle of proglottid. Eggs not seen.

Host: Hypoprion brevirostris.
Location: Spiral valve.
Locality: Dry Tortugas, Florida.
Type: U. S. N. M. No. 9063.

Discussion: The hooks of *Tentacularia pseudodera* resemble most closely those of *T. speciosa* (Linton, 1897), a larval form. Linton describes similar small hooks which, however, are not arranged in definite longitudinal rows. There are none of the larger hooks with elongated bases as described for *T. pseudodera.* The larger S-shaped hooks are not arranged in groups of six in *T. speciosa.* The sizes of the scolex and hooks are closely correlated in both forms, however.

Yamaguti (1934) referred Linton's species to a new genus which he named Lintoniella. He says: "For *Rhynchobothrium speciosum* Linton, 1897, characterized by the proboscis hooks, I propose a new genus Lintoniella." He gives no generic diagnosis or description, however, and therefore leaves no basis for determining whether *T. pseudodera* belongs in the genus *Lintoniella.* Therefore, for the present at least, the genus *Tentacularia* is being used for this species.

T. pseudodera differs from *T. perelica* markedly in the character of the hooks (those of the former being consistently smaller) as well as in the total size of the scolex. They differ also in the general character of the scoleces, the "false neck" of *T. pseudodera* being distinctive. The brackets in the proboscis sheaths are much the same in both species, as is shown in figures 6 and 8.

The name *pseudodera* is from *pseudo:* false; and *dera:* neck, and refers to the body constriction near the bases of the bulbs.

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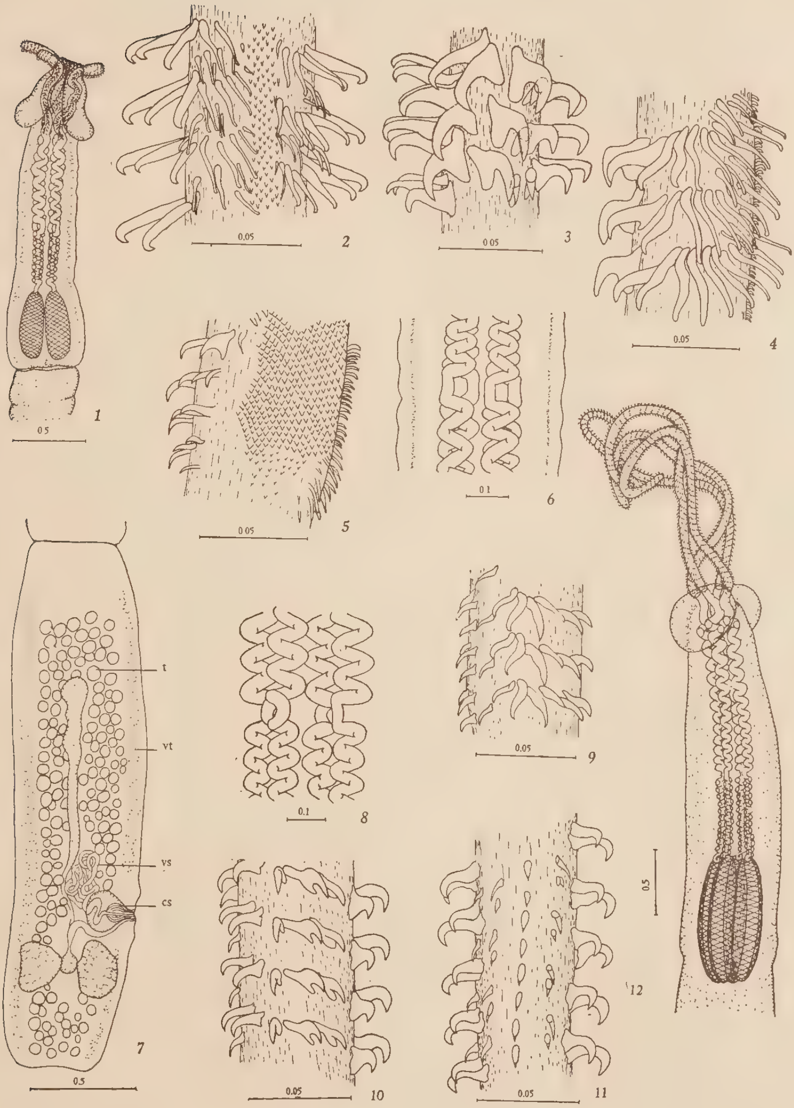
Explanation of Plate

All figures were drawn with the aid of a microprojector or camera lucida. The value of the projected scale is indicated in millimeters beside each figure. The following abbreviations were used:

cs—cirrus sac
t —testis
vs—vas deferens
vt—vitelline glands

Fig. 1. *Tentacularia perelica.* Scolex, lateral view.
Fig. 2. *T. perelica.* Proboscis, outer side.
Fig. 3. *T. perelica.* Proboscis, inner side.
Fig. 4. *T. perelica.* Proboscis, lateral side.
Fig. 5. *T. perelica.* Base of proboscis, outer side, showing scales.
Fig. 6. *T. perelica.* Section of scolex showing "brackets."
Fig. 7. *T. perelica.* Mature proglottid.
Fig. 8. *T. pseudodera.* Section of scolex showing "brackets."
Fig. 9. *T. pseudodera.* Proboscis, lateral side.
Fig. 10. *T. pseudodera.* Proboscis, inner side.
Fig. 11. *T. pseudodera.* Proboscis, outer side.
Fig. 12. *T. pseudodera.* Scolex, ventral view.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NATURAL TRANSMISSION OF IMMUNITY AGAINST *TRYPANOSOMA LEWISI* FROM MOTHER RATS TO THEIR OFFSPRING

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The natural transmission of immunity from mother animals to their offspring is of such fundamental importance in biology and medicine that it has been extensively investigated from the early years of the study of immune phenomena. (Famulener; Guyer and Smith; Needham; Rodolfo.) Relatively few reports have been offered upon the transfer from mother to offspring of resistance against animal parasites. Miller has noted that the young of specifically immunized mother rats resist infection with onchospheres of *Taenia taeniaeformis,* and Shorb has reported that the young of resistant mother mice and rats are resistant to *Hymenolepis fraterna* during the period of nursing. Very little attention has been directed toward the possible transfer of acquired immunity against protozoan infections. Recently, Minning reported that immunity against *Trypanosoma lewisi* is not passed from mother rats to their offspring, and Collier obtained the same result in a study of *Trypanosoma cruzi* in white mice; but Schilling, on the other hand, has suggested that the transfer of resistance against *Trypanosoma brucei* and *Trypanosoma congolense* does occur.

It seemed probable that the fundamental principles underlying the immunity against the protozoan infections are essentially the same as against other infectious agents and that a study carried out with *Trypanosoma lewisi* in rats might throw some light on the entire question of transfer of immunity from mother to offspring. This parasite, which is found naturally in the wild rat, can be transferred to laboratory strains of rats easily, giving rise quite regularly to heavy infections. The adult rat nearly always recovers from its infection and—what is of paramount importance for the present study—shows thereafter a powerful and lasting immunity. Perhaps it is necessary to mention that in this infection in the normal susceptible rat, several apparently distinct antibodies are developed. The first makes its appearance about the fifth or sixth day after infection and functions to prevent multiplication of the parasites which, till that time, are multiplying with tremendous rapidity. Between the seventh and tenth day, usually, there is a crisis in the parasite num-

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ber, which probably results from the elaboration of a lytic antibody. However, the action of this lytic substance is generally incomplete and a small number of parasites persist in the blood for from a few days to six weeks thereafter. Finally, all parasites are lost suddenly in a crisis caused by the rather explosive appearance of another lytic antibody, and the animal is thereafter immune to reinfection. The reproduction-inhibiting antibody is probably present throughout the remaining lifetime of the animal and is primarily responsible for its resistance. The lytic substance disappears in a few days after the parasites have been lost, although it can be called forth again under suitable stimuli. (Taliaferro, 1926.)

The rat seemed to be a quite favorable animal to employ for the study of natural transfer of immunity from mother to offspring since it is easily mated in the laboratory, produces litters of considerable size after a brief gestation period (21 days), and tolerates division and substitution of litters and the handling of its offspring, all of which procedures are necessary to such an investigation.

We undertook, therefore, a study designed to determine, first, whether specific immunity against *Trypanosoma lewisi*[1] is transferred naturally from mother rats to their offspring. Then, after such transfer was found to occur, we endeavored to learn the exact method of transfer, as well as other relevant considerations of the immunity which is thus conferred on the young.

THE TEST FOR IMMUNITY IN THE YOUNG OF MOTHER RATS IMMUNIZED TO *Trypanosoma lewisi*

In the first experiment, the courses of infection were compared in two successive litters from the same mother, one delivered before and the other after the mother rats had been infected with *T. lewisi*. Mothers number 415 and 418 were used for this purpose. Mother 415 had produced a litter of 9 young on January 12. On February 2, after the usual 21-day nursing period, she was removed from the young, injected intraperitoneally with 1,000,000 *T. lewisi,* and placed in a mating cage for one week. The infection in this female ran the usual course and she was free of parasites on February 27, when 3 young were delivered. Mother 418 produced a normal litter of 10 young on January 14, and was removed to a mating cage on February 4, after being injected that day with 1,000,000 *T. lewisi.* The infection in this rat ran the usual course and the animal was negative on March 1, when 5 young were born.

[1] The strain of *Trypanosoma lewisi* used in this work was obtained from Dr. L. Reiner of the Burroughs Wellcome and Company, Tuckahoe, New York. The strain of *Trypanosoma cruzi* was given by the late Professor J. G. Thomson, of the London School of Hygiene and Tropical Medicine.

The two litters of each female were infected at intervals, beginning about 10 days after delivery, with 1,000,000 *T. lewisi,* given intraperitoneally. Every young rat of the litters which were produced before the mother had been infected was readily susceptible to infection with *T. lewisi,* the younger forms of mother 418 dying of their infection. On the other hand, none of the young produced after the mothers were immunized by infection could be infected during the first 29 days after birth. In fact, only one parasite was seen in the resistant animals at any time, and this on the fifth day after the injection of one animal. The tail blood of all animals was examined daily (50 high-dry fields of the microscope) for 15 days following the inoculation. It was indicated from this work that the protective substances elaborated by the mother as the result of infection with *T. lewisi* were transferred to the offspring.[2]

a. *The persistence of the immunity against* Trypanosoma lewisi *which is transferred from mother rats to their offspring.* It was important to know how long after birth the offspring of an immune rat *retained* its immunity to *T. lewisi,* especially since it is well known that a rat actively immunized by infection with *T. lewisi* remains immune for long periods after recovery, in some cases possibly for life. The young which were produced after mothers 415 and 418 had been immunized were, therefore, kept until they were about 45 days old, then reinjected with 1,000,000 *T. lewisi.* On examination two days after the injection, every animal was found to be infected, although the intensity of the infections which developed in subsequent days differed between wide limits. Rat number 12–2 (Table 1), for example, behaved essentially as a normal animal, the infection showing, on the fourth day after the inoculation, 200,000 parasites per cu mm of blood and persisting for 16 days. In contrast, rat number 12–3 showed no more than 2 parasites per fifty fields on the third, fourth, and fifth days after inoculation and, thereafter, was consistently negative. It appears from this experiment that the immunity of the young of an immune mother rat is, in contrast to that of the mother animal herself, definitely temporary.

THE MODE BY WHICH THE YOUNG OF IMMUNE MOTHERS ACQUIRE IMMUNITY TO *Trypanosoma lewisi*

Having shown that the young of immune mother rats were also immune to *T. lewisi,* it then became necessary to determine how the young

[2] All of the rats used in this work were of the Sherman strain, which has been kept for some years by the Department of Animal Care of this College. They were fed a diet consisting of hulled oats, whole corn, yellow corn, shelled barley, soy-bean meal (of each 15%), powdered whole milk (10%), Swift's commercial dried meat scraps (10%), green alfalfa meal (2%), sodium chloride (2%), and calcium carbonate (0.5%). This mixture was prepared at 2 week intervals of freshly ground ingredients. The diet was devised by Dr. C. A. Slanetz and has been used for breeding rats and lactating mothers for 7 years in the Department of Animal Care.

TABLE 1.—*Demonstrating resistance against* T. lewisi *of litters of rats produced by immune mothers compared with susceptibility of litters produced prior to immunization of mothers. After about 45 days, the resistant young become susceptible*

Mother rat No.	Litters produced prior to immunization of mothers: Young rat No.	Age (days) when young rat was injected with 1,000,000 *T. lewisi*	Maximum hemacytometer count, parasites per cu mm (day of infection in parentheses)	Litters produced after immunization of mothers: Young rat No.	Age (days) when young rat was injected with 1,000,000 *T. lewisi*	Result (50 high-dry fields observed daily for 15 days)	Age (days) when reinjected with 1 mil. *T. lewisi*	Observation on designated days after reinjection with 1,000,000 *T. lewisi*: 2	3	4	6	9
	1–1	11	540,000 (7)	2–1	11	0	46	+	+	30,000	0	0
	1–2	18	525,000 (7)	2–2	16	0	46	+	++	+	+	0
	1–3	25	276,000 (3)	2–3	21	0	46	+	++	+	0	0
415	1–4	32	820,000 (9)									
	1–5	39	1,010,000 (7)									
	1–6	46	240,000 (7)									
	1–7	53	800,000 (10)									
	1–8	60	263,000 (7)									
	11–1	9	Dead from infection (7)	12–1	9	0	44	+	++	++	+	0
	11–2	16	" " " "	12–2	14	0*	44	+	++	200,000	−	++**
	11–3	23	266,000 (3)	12–3	19	0	44	+	+	+	0	0
418	11–4	30	580,000 (7)	12–4	24	0	44	+	++	90,000	150,000	++**
	11–5	37	740,000 (6)	12–5	29	0	44	+	++	50,000	40,000	++**
	11–6	44	360,000 (12)									
	11–7	51	440,000 (9)									
	11–8	58	130,000 (7)									

* One parasite seen in one of 50 high-dry fields on the fifth day only after the injection.

\+ Less than 1 parasite per high-dry field ; ++ from 1 to 10 parasites per high-dry field ; hemacytometer counts made when more than 10 parasites occurred per high-dry field.

** Rat 12–2 remained positive for 16 days after reinjection, and rats 12–4 and 12–5 were positive for 11 days after injection.

acquired their immunity. It was possible that the young suffered an infection *in utero,* the parasite passing the placental barrier, and were thus actively immunized. Or, if this were not the case, there remained two possible channels for passive transfer of the mother's protective substances—namely, through the placenta and through the milk. Finally, it was possible that the immunity of the young was essentially non-specific, and was not governed by the same principles which control the immunity induced by artificial transfer of the serum of an immunized rat. The results of experiments undertaken to elucidate these points are next presented.

a. *Test to determine whether* Trypanosoma lewisi *can pass the placental barrier.* In order to determine whether the resistance of the young of immune mothers was acquired actively as the result of infection of these young during residence in the uterus of the infected mother, it was necessary to find whether *T. lewisi* could pass the placental barrier. For this purpose, four pregnant rats all near the end of their gestation period, were injected with 1,000,000 *T. lewisi.* One of these was permitted to deliver her young normally. Although there was one parasite per high-dry microscope field of the mother's blood on the day of parturition and larger numbers (up to 75 per field) subsequently during the period of nursing, the young showed no organisms whatsoever at any time in the 10 days after birth during which their tail blood was examined. The three remaining pregnant females were killed prior to delivery at a time when their tail blood showed many parasites. The embryos were carefully removed from the uterus and placed in water at 37° C. The placenta was removed, sliced open with scissors, and its blood examined. Trypanosomes were abundant in the placental blood. Blood from the umbilical cord and from the fetal heart were then observed microscopically but no parasites whatsoever were seen. These observations were repeated upon each of the embryos from each female, with identical results.

It is clear from these observations that *T. lewisi* is not able to pass the placental barrier or, in agreement with an earlier observation of Fine upon *T. brucei,* to infect the young through the milk. The immunity of the young of immune mothers is, therefore, a passive immunity, protective substances being transferred naturally from the mother to the offspring.

b. *Test whether young must be* in utero *during the mother's infection in order to receive protective substances from the mother.* Rats which recover from an infection with *T. lewisi* are possibly immune to this parasite for their remaining life. It was significant to determine whether litters produced from a mating effected after mothers had re-

covered entirely from their infection received from these mothers protective substances against *T. lewisi.* In others words, it was necessary to find whether the young must be *in utero* during the mother's infection in order to be protected against the parasite.

Two female rats, numbers 415 and 418, which had delivered susceptible litters before their infection, and had delivered immune litters about the time their blood stream had cleared itself of parasites, were mated a third time after the disappearance of parasites from the peripheral blood. Mother 418 delivered three young 47 days after the mother's recovery. After nursing this mother for 4 days, these young were injected with 1,000,000 *T. lewisi.* Two of the three young proved wholly resistant, no trypanosomes being seen during the ensuing 15 days. The third showed 1, 4, and 2 parasites in 50 high-dry microscope fields on the second, third, and fourth days respectively after infection, and none thereafter. Only two of the young which mother 415 delivered 73 days after she had recovered from infection were nursed by this mother, and these were injected with 1,000,000 *T. lewisi* when one day old. Although both showed some organisms, neither showed a significantly large number of parasites during the ensuing 15 days and were, therefore, considered resistant to the infection.

It is shown by this experiment that the young need not be present in the mother's uterus during her infection in order to receive protective substances from her, since litters produced at least 73 days after the mother's infection had disappeared were protected against 1,000,000 parasites injected 1 day after birth. Stated otherwise, the mother was still able to transfer her resistance to young which she delivered at least 73 days after she had completely recovered from her infection. Nevertheless, from data presented later, it is strongly suggested that the power of the mother to confer resistance to her offspring diminishes with time after she has recovered from infection, and that the young are best assured of resistance if they are in the uterus during the mother's infection and nurse the mother very soon after she has recovered.

c. *The route by which protective substances are transferred from mother to offspring.* There are but two possible channels for passive transfer of protective substances from mother to offspring—namely, through the placenta or, after birth, through the milk. In order to find which of these channels is the significant one in the natural transfer of immunity from mother to offspring, part of the new-born litter of an immune mother rat was interposed with part of the new-born litter of a normal mother. Great care was exercised to prevent the young from nursing their mothers until the parts of the litters were interposed. When the exchange of young was effected—within an hour after birth—no milk could be seen in the stomach through the abdominal wall. This

experiment was carried out three times, part of the young of immune mothers 528, 415, and 418 being interposed with those of normal mother rats. In the experiment involving the young of mother 528, which had recovered from infection on the day of delivery, the young were injected with 1,000,000 *T. lewisi* on the day of birth. All of the offspring of the immune mother—the 5 nursed by her and the 3 nursed by the normal mother—were completely resistant to infection, no parasites being seen in their blood at any time. Of the four young of normal mother 561 which were nursed by immune mother 528, two proved wholly resistant and two showed a relatively low-grade infection: one of those infected exhibited only 1 parasite in 50 high-dry fields of the microscope on the first and third days after the injection, and the other experienced a reasonably heavy infection which was overcome after 6 days. The normal young nursed by the normal mother proved readily susceptible to infection and were dead of their infection by the fifth day following the injection, with large numbers of trypanosomes present in the blood.

Part of the litter of immune mother 415, which recovered from her infection 73 days before this delivery, was interposed with part of the young of normal mother 580. All the young were injected with 1,000,000 *T. lewisi* when they were 1 day old. The two young of immune mother 415 nursed by this female were definitely resistant, one showing very few parasites irregularly for six days and the other showing only 1 parasite in 50 microscope fields on the fifth day after the injection. The normal young nursed by the immune mother were also relatively resistant when compared with others of the same litter nursed by their own (normal) mother. Nevertheless, 2 of the 5 normal young nursed by the immune mother experienced a somewhat heavy infection lasting 16 days. The young of the immune mother which were nursed by the normal mother all experienced slightly lighter infection than the normal young nursing the normal mother, yet a definitely heavier infection than the normal young nursing the immune mother.

Parts of the litters of immune mother 418, which had recovered 47 days before this delivery, and normal mother 800 were also interposed. The young were injected with 1,000,000 *T. lewisi* when four days old. Of those nursed by mother 418, 2 of 3 born of this immune mother were completely resistant and the third showed only a very light infection for three days; 2 of 3 born of the normal mother developed heavy infections (one ending fatally), and the third had a very slight infection manifested only on the second day. Of the young nursed by normal mother 800, 2 born of this mother experienced heavy infections from which they recovered after 17 and 22 days respectively, and 3 born of the immune mother also developed intense infections, 2 of which ended fatally. In this case, as with mother 415, the mother had only limited capacity com-

pared with immune mother 528 to transfer protective substances, since one of her own young nursed by herself proved susceptible to infection. It is notable that an earlier litter by this mother delivered on the day she recovered from her infection was distinctly more resistant.

The results of this work, the data of which are presented in Table 2, show that the protective substances against *T. lewisi* are transferred from mother rats to their offspring both through the placenta and through the milk. It is further indicated that the more secure protection is conferred by mothers which have recovered from infection only a short time prior to delivery. The fact that young rats born of normal mothers but nursed from birth on an immune mother are able to resist 1,000,000 *T. lewisi* injected on the first day of life indicates not only that the first milk (colostrum) is rich in the protective antibody, but also that the intestine of the new-born rat must be highly permeable to this antibody after it is ingested. Evidence is provided from the young mothers 415 and 580 that a greater amount of protective antibody is transferred to the young through nursing upon an immune mother for 1 or 2 days than through residence in the uterus of this immune mother during the entire gestation period. It is evident from the course of infection seen in the young of immune mothers nursed on normal mothers 580 and 800 that the immunity passed through the placenta does not serve to protect the young for many days after birth. Nevertheless, it must be recognized that the capacity to transmit protective substances either by placenta or milk depends primarily upon their presence in the mother's blood. Immune mothers recently recovered from their infection (*e.g.*, No. 528) are able to transmit by either route sufficient antibody to protect the young completely for a considerable interval, as the experiment with the young of immune mother 528 shows.

1. *The relative persistence of the immunity acquired by the young of a normal mother rat which nurse upon an immune mother.*

It was of interest to compare the young of an immune mother with those of a normal mother in respect to the persistence of the immunity acquired through nursing upon the immune mother. For this purpose, the young were injected with 1,000,000 *T. lewisi* at intervals after they had begun to nurse the immune mothers, immune mothers number 528 and 418–73 being used for the purpose. All of the young with mother 528, save number 5, proved resistant for the first 25 days after birth. They were permitted to rest for 35 days, then were reinjected with 1,000,000 *T. lewisi*. All but one animal, number 8, became infected, although some others, particularly the young of the normal mother, showed only a low-grade infection from which they quickly recovered. In the case also of those with immune mother 418–73, most rats became infected, although the normal young which nursed this immune mother sustained

TABLE 2.—*Demonstrating that protective substances are passed from immune mothers to young by way of both placenta and milk*

Young rat No.	Born of mother No.	Nursed upon mother No.	Observations on designated days after infection with 1 million *T. lewisi*															
			1	2	3	4	5	6	7	8	9	10	12	15	17	20	22	23
1	528 (immune)	528 (immune)	0	0	0	0	0	0	0	0								
2			0	0	0	0	0	0	0	0								
3			0	0	0	0	0	0	0	0								
4			0	0	0	0	0	0	0	0								
5	561 (normal)		+	+	2+	3+	3+	+	0	0								
6			+	0	+	0	0	0	0	0								
7			0	0	0	0	0	0	0	0								
8			0	0	0	0	0	0	0	0								
9	528 (immune)	561 (normal)	0	0	0	0	0	0	0	0								
10			0	0	0	0	0	0	0	0								
11			0	0	0	0	Dead*											
12	561 (normal)		0	+	2+	4+	4+	Dead										
13			+	+	2+	4+	Dead											
14			+	+	2+	4+	4+	Dead										
1	415 (immune)	415 (immune)	+	0	+	0	+	+	0	0	0	0						
2			0	0	0	0	+	0	0	0	0	0						
3	580 (normal)		0	+	+	+	0	Dead*										
4			+	0	+	+	+	+	+	0	0	0						
5			+	+	+	2+	4+	4+	4+	4+	4+	4+	2+	+	0			
6			+	+	+	+	+	+	+	+	0	0						
7			0	+	+	+	+	2+	2+	3+	3+	3+	2+	0	0			
8	415 (immune)	580 (normal)	0	+	+	+	+	2+	3+	3+	4+	4+	2+	+	0			
9			+	2+	2+	2+	3+	3+	3+	3+	4+	4+	3+	2+	0			
10			+	+	2+	3+	3+	3+	4+	3+	3+	3+	2+	+	+			
11	580 (normal)		+	2+	2+	3+	4+	4+	3+	3+	4+	4+	3+	2+	2+	+	0	0
12			+	2+	2+	3+	4+	4+	3+	4+	4+	4+	3+	2+	2+	0	0	
13			+	+	2+	3+	4+	4+	4+	4+	3+	3+	3+	2+	2+	0	0	
1	418 (immune)	418 (immune)	0	0	0	0	0	0	0	0	0	0						
2			0	0	0	0	0	0	0	0	0	0						
3			0	+	+	+	0	0	0	0	0	0						
4	800 (normal)		+	+	2+	2+	3+	3+	4+	3+	4+	4+	Dead					
5			0	+	2+	3+	3+	3+	3+	3+	4+	4+	3+	3+	2+	0	0	
6			0	+	0	0	0	0	0	0	0	0						
7	418 (immune)	800 (normal)	0	2+	3+	4+	3+	4+	4+	4+	4+	Dead						
8			0	+	3+	4+	3+	3+	4+	4+	4+	4+	4+	4+	2+	2+	+	0
9			0	+	3+	4+	4+	4+	4+	4+	4+	4+	Dead					
10	800 (normal)		+	+	3+	4+	3+	4+	4+	4+	4+	3+	2+	2+	+	+	0	0
11			0	+	3+	4+	4-	4+	4+	4+	3+	3+	2+	+	0			

* Died of intercurrent infection. No trypanosomes in blood at time of death.
Key: 0 = no parasites in 50 high-dry fields; + = less than 1 parasite per field; 2+ = 1 to 10 parasites per field; 3+ = 10 to 50 parasites per field; 4+ = over 50 parasites per field.

somewhat heavier infections than her own progeny. Even so, some of the normal young here also proved wholly resistant. The data are presented in Table 3.

It is shown from this work that the immunity acquired by normal young through nursing upon an immune mother is about as secure and as enduring as that acquired by the young born of and nursed by that mother, and that through nursing such a mother normal young have about as great chance of surviving an injection with the parasite as the own young of that immune mother. In any case, the resistance carries well past the milk-feeding period and in some instances till the rat reaches at least two months of age.

One further point is brought out by the data in Table 3. Normal rat number 5, nursed on immune mother 528, sustained a somewhat heavy infection after the initial injection of trypanosomes, as many as 25 parasites per field being observed on the fourth day post-injection. The infection lasted in this animal only seven days. This rat proved susceptible to reinfection on reinjection at 60 days of age, despite its earlier infection, although the second infection lasted only two days. Apparently the initial infection was not sufficiently intense to confer a lasting complete immunity, although the animal was able as a result of its first experience to respond more readily than its mates to a later infection. Similarly, rat number 7, in which only a very slight infection was experienced after the initial injection of parasites, also showed only a very mild infection lasting four days after reinjection when 60 days old.

d. *The acquisition of immunity by young from a mother which develops protective antibody after parturition.* Two pregnant rats were infected with *T. lewisi* a short time before parturition. One of these, number 700, delivered her litter the day after being injected and showed parasites in the tail blood for the first time 2 days after the delivery. The peak of the rather low-grade infection in this female was reached five days later, when the young were 7 days old, at this time from 8 to 10 parasites being found per high-dry microscope field. Four days later, this mother was free of infection. The other pregnant rat, number 701, was positive for the infection four days after injecting the organisms and on the next day, when six young were delivered, showed 1 parasite per high-dry field. The infection in this animal became quite intense, a peak of 75 parasites per field being attained on the seventh day after parturition. The young of these two mother rats were injected at intervals during the nursing period to see whether antibody acquired after parturition is transferred to the young.

One of the 4 young of mother 700 was injected with 1,000,000 *T. lewisi* when six days old and one day before the peak of the mother's infection was reached. The infection developed rapidly in the young

TABLE 3.—*Demonstrating persistence of acquired immunity in young born of normal mother and young born of immune mother, all nursed upon immune mother*

Young rat No.	Born of mother rat No.	Nursed by immune mother rat No.	Trypanosomes observed in daily observations after injecting 1 mil. *T. lewisi* when 1, 10, 20, and 25 days old	Trypanosomes observed on designated days after reinjection of 1 mil. *T. lewisi* when 60 days old					
				1	2	3	4	5	6
1	528 (immune)	528	0	+	2+	2+	3+	4+	3+
2			0	+	2+	2+	2+	0	0
3			0	+	2+	3+	4+	4+	4+
4			0	+	2+	3+	3+	3+	3+
5	561 (normal)		*	+	2+	0	0	0	0
6			0	+	2+	3+	3+	3+	3+
7			*	+	2+	+	+	0	0
8			0	0	0	0	0	0	0
11	418–73 (immune)	418–73	0	0	0	+	0	0	0
12			0	0	0	0	0	0	0
13			0	0	+	0	0	0	0
91	702 (normal)		0	2+	2+	2+	2+	+	0
14			0	0	0	0	+	2+	3+
15			0	+	2+	3+	3+	4+	4+

* Rat No. 5 experienced a rather intense infection for ten days, and Rat No. 7 was positive on 2 days after initial injection (for details, see Table 2). Both were negative after reinjection when 10, 20, and 25 days old.

Key to observations: same as Table 2.

rat to a fatal end 7 days later. The three remaining young were injected when 13 days old, two days after the mother had completely recovered. While all of these young became infected, showing as many as 1 parasite per high-dry field of the microscope on the second day, the infections quickly subsided and had entirely disappeared by the seventh day.

Two of the young of mother 701 were injected three days before the peak of the mother's severe infection. Both of the young showed severe infections, but these quickly subsided after the fourth day, when the infection in the mother also was diminishing, and both were negative by the twentieth day. Two other young of this litter were injected with 1,000,000 *T. lewisi* four days after the peak of infection in the mother was reached. Both of these young suffered only a very low grade infection which was negative by the seventh day. The final two young of mother 701 were injected with 1,000,000 *T. lewisi* on the day that the mother was first found to be free of infection. Neither of these young showed any parasites at any time after the injection.

It is shown by the data obtained from this experiment, which are given in Table 4, that the antibody developed by the mother rat after parturition is secreted in the milk and protects the young which ingest the milk.

e. *The capacity of the intestine of normal young rats of different nursing ages to absorb protective substances against* T. lewisi *from the milk ingested from an immune mother.* The new-born normal young nursed by an immune mother were found to be resistant to infection when injected with 1,000,000 *T. lewisi* one day later. It seemed possible that the intestine of young rats might quickly lose its initially great permeability. Therefore, in one experiment, a normal litter of rats were transferred at intervals to nurse upon an immune mother, 2 being transferred when new-born, and 2 at 4, 2 at 9, and 3 at 11 days of age. In another experiment, pairs of the young of normal mothers—2 new-born and 2 each 5, 10, and 15 days old—were transferred to a lacating immune mother. After nursing for 24 hours, all were injected with 1,000,000 *T. lewisi,* then permitted to continue nursing upon the immune mother. Although examined daily for 15 days after the injections, none of the rats showed trypanosomes at any time.

It is shown from this experiment that the intestine of normal nursling rats continues to be permeable to the protective antibody ingested in the milk from immune mothers during at least the first 15 days after birth. It is also indicated that not only the colostrum but the milk secreted later by an immune mother contains sufficient antibody to confer protection to young normal rats which ingest the milk.

TABLE 4.—*Transfer of immunity through milk to young from mother rat which developed protective antibody after parturition*

Mother rat No.	Mother injected with 1 mil. *T. lewisi*	Course of infection in mother			Young born	Young rat No.	Young infected with 1 mil. *T. lewisi*	Age (days) of young when infected	Observations upon young on designated days after their infection													
		Appeared	Peak	Cleared					1	2	3	4	5	6	7	8	9	10	12	14	16	18
700	4/26	4/29	5/4	5/8	4/27	1	5/3	6	+	2+	4+	4+	4+	4+	Dead							
						2	5/10	13	+	2+	2+	2+	+	+	0	+	+	0	0	0	0	0
						3	5/10	13	+	+	+	+	+	0	0	0	+	0	0	0	0	0
						4	5/10	13	+	+	+	+	0	+	0	0	0	0	0	0	0	0
701	4/24	4/28	5/6	5/19	4/29	1	5/3	4	+	3+	3+	4+	3+	3+	2+	2+	2+	+	+	+	+	0
						2	5/3	4	+	2+	3+	3+	3+	2+	3+	2+	+	+	+	+	0	0
						3	5/10	11	+	+	+	+	+	+	0	0	0	0	0	0	0	0
						4	5/10	11	+	+	+	0	+	0	0	0	0	0	0	0	0	0
						5	5/19	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
						6	5/19	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Key to observation: same as Table 2.

THE SPECIFICITY OF THE IMMUNITY CONFERRED FROM MOTHER RATS TO THEIR OFFSPRING

It seemed possible that the immunity demonstrated by the foregoing experiments could be explained through the transfer to the young of some non-specific substance, possibly of the character of a hormone or enzyme, and that the protective agency here involved differed from that to which the mother herself owed the immunity she acquired by recovery from infection. However, if the immunity of the young were specific, it would seem the same antibody to which the mother owes her resistance is responsible for the immunity of the offspring. In order to test the specificity of the transferred immunity, three of a litter of seven young born of mother 900, which was immune to *T. lewisi,* were injected when 7 days old with 1,000,000 *T. lewisi,* and the remaining four young were injected with a suspension of *T. cruzi.* At no time subsequently were trypanosomes observed in the three young injected with *T. lewisi,* the immunity against the specific form being complete. However, *T. cruzi* was observed in the blood of the four young injected with this form as early as the third day thereafter and, as is usual in the progress of this infection in young rats, the number of parasites rose sharply after the tenth day. Three of these animals died on the fifteenth day of the infection and the fourth, also very heavily infected, was then disposed of (see Table 5).

It is indicated from this result that the immunity against *T. lewisi* which is transferred from the recovered mother rat to her offspring is specific, at least that it is not effective against a closely related species of trypanosome. The author with Kolodny has recently shown that the serum of rats recovered from infection with *T. lewisi* likewise is without effect in preventing infections with *T. cruzi.* It is probable that the resistance which is transferred from mother to offspring depends upon the transfer of the serum globulin containing the antibody (Taliaferro, 1932) from the mother to the young by way of both the placenta and the milk.

DISCUSSION

The natural infection of wild rats with *T. lewisi* is of cosmopolitan distribution and has an incidence of 25 per cent or more in the rat population of many localities. In adult laboratory rats, and probably likewise in adult wild rats, the infection is relatively nonpathogenic, and even when intense elicits no symptoms. However, very young laboratory rats, in the writer's experience, are not infrequently killed by infection with this form. In fact, from 50 to 100 per cent of the members of some normal litters which have been injected in this laboratory when 10 days old have succumbed.

TABLE 5.—*Demonstrating specificity of immunity against* T. lewisi *transferred from mother rats to offspring*

Young rat No.	Trypanosome injected	Age (days) of young rat when injected	Number of trypanosomes counted in 50 high-dry fields on designated days after injection of trypanosomes											
			3	4	5	6	7	8	10	11	12	13	14	15
1	*T. lewisi*	7	0	0	0	0	0	0	0	0	0	0	0	
2	" "	7	0	0	0	0	0	0	0	0	0	0	0	
3	" "	7	0	0	0	0	0	0	0	0	0	0	0	
4	*T. cruzi*	7	4	5	1	14	11	4	30	172	90	335	555	*
5	" "	7	8	9	0	18	8	17	58	157	270	315	775	*
6	" "	7	4	1	4	6	4	13	56	80	90	255	455	*
7	" "	7	4	8	5	13	26	8	67	75	65	195	480	–

* Dead of infection.
All young were in the same litter from immune mother 900 and nursed by the mother throughout the period of observation.

The results of the experiments presented in this paper probably explain why natural infection with this common parasite of rats does not usually occur in very young rats, but only in those animals which are well along toward adulthood and able to shift for themselves. If a mother rat were to develop an infection with *T. lewisi* in the first days after she delivered her litter, infection of her young by way of the fleas in the nest would be practically inevitable with, probably, a fatal end for some of the litter. But if the mother is herself immune at the time of delivery, or has been infected for a sufficient time to have begun forming antibody to protect herself against the parasite, the chance for the young to survive the infection and even to escape infection altogether will be high, for the antibody of the mother will be both passed through the placenta and secreted in the mother's milk and absorbed by the young rat from its intestine. As our experiments with laboratory rats show, this protection is a temporary one and there is every reason to suspect the young of an immune mother wild rat also lose their passively acquired resistance as they grow older and, sooner or later, suffer an acute infection with this parasite. Yet the protection acquired from the mother will persist until the young rats are well past the age when an infection would result fatally and until the chances of their survival are quite favorable by reason of their own powers of antibody production.

No effort was made to determine the exact functional character of the antibody transferred to the young. Probably its character depended upon the character of the antibody in the immune mother at parturition and during the nursing period. It is likely that, if the mother had recovered from her infection just prior to delivery, both the lytic antibody and the reproduction-inhibiting antibody were transferred, but if recovery had occurred several weeks or more before delivery, only the reproduction-inhibiting antibody would be available in the mother for transfer to the young. This may explain why, particularly in the young of mothers recovered for considerable intervals, low-grade infections persisted for about one week, with no appreciable increase in the number of parasites during this interval. In these cases, the animals were receiving the reproduction-inhibiting substance from the mother but no lytic antibody to get rid of those few trypanosomes which had been able to develop. The final disappearance of these forms from the young can probably be explained through the elaboration by the infected young animal itself of a specific lytic substance.

In a number of cases, one or more normal young, although nursing an immune mother, failed to manifest the resistance shown by its litter mates nursing the same mother, and experienced an infection quite like that of normal young nursed upon a normal mother. While no explanation for this failure to acquire immunity is apparent, it is possible that

had these young nursed the immune mother for a longer period before being infected, they, too, would have proved resistant, since a greater amount of milk would have been ingested and more antibody absorbed. In those young which failed to exhibit resistance, the infection may simply have gained so much headway before the ingested antibody became available to protect, that despite its presence and its continuous supply thereafter, the multiplication of the trypanosomes could not be significantly curbed.

SUMMARY

The young of mother rats which have recently recovered from an infection with *T. lewisi* are for the first few weeks of life immune to infection with this parasite. The resistance of the young depends upon the passive transfer to them from the mother of specific protective antibodies. These antibodies are transmitted in part by way of the placenta and in part by the milk. In the experiments here reported, the mother has been able to transfer protective substances to the young for at least 73 days after her recovery from infection, and probably strongly resistant mothers could do so for considerably longer periods. It is, definitely, not necessary that the young be *in utero* during the mother's infection in order to be resistant. The immunity of the young is not the result of active infection of the young *in utero* or during the nursing period because *T. lewisi* is unable to pass to the young either through the placenta or the milk.

The young of normal mothers which are placed to nurse upon immune mothers promptly become resistant. If the mother be herself highly immune, she can confer to new-born normal young rats within 24 hours sufficient antibody through her milk to render them at one day of age wholly resistant to an injection of 1,000,000 *T. lewisi.*

Immune mother rats secrete the protective substances not only in the colostrum, but also in the milk later passed, and young rats which suckle upon an immune mother are able to absorb from their intestine the antibody they ingest in the mother's milk for at least 15 days after birth. Young rats born of and nursed by a normal mother become immune if the mother become infected and develop antibody during the nursing period after parturition.

The immunity transferred from mother to offspring is specific, and the young of a mother immune to *T. lewisi,* although resistant to *T. lewisi,* are as susceptible as normal young to *T. cruzi.*

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ACQUIRED IMMUNITY IN RATS AGAINST *TRYPANOSOMA CRUZI**

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Comparatively little research has been reported on the immunity of animals against *Trypanosoma cruzi,* the organism which causes the human infection of the American tropics known as Chagas' disease. This parasite differs from nearly all other mammalian trypanosomes in that it multiplies not in the blood stream but within the cells of the fixed tissues, especially in the striated muscle fibers. It seemed possible that, because the reproduction of the parasite goes on outside the blood stream, the immunological responses which an infected animal makes against it would differ from those against *Trypanosoma lewisi,* a form confined to the blood stream, and with which *Trypanosoma cruzi* is usually linked taxonomically. We have, therefore, studied the infection of rats with *Trypanosoma cruzi,* first to determine whether rats acquire immunity through recovery from an infection with the parasite, and, subsequently, whether the injection of serum from such rats confers protection to normal rats or provides an effective mode of treating infected rats.

PROCEDURE AND RESULTS

a. *Active immunity against* Trypanosoma cruzi *in rats.* Several young rats were injected with 0.1 cc of the citrated blood from a seed rat harboring *Trypanosoma cruzi.* Between the second and third week following, the injected rats proved to be infected, on tail blood examination, and continued to show their infection without interruption for 3 weeks, and intermittently for two weeks longer. Thirty-five days after the parasites were last observed in the blood of any of these animals, the rats were reinjected with *Trypanosoma cruzi,* a number of organisms about equal to that first given being administered. No organisms were found in the blood of these animals at any time during the 36 days subsequently that they were examined. Apparently the animals were, as the result of recovery from their initial infection, able to resist wholly the reinfection. The details of this study upon three animals are presented in Table 1.

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* The strain of *Trypanosoma cruzi* was supplied to me in the insect host, *Rhodnius prolixus,* by the late Professor J. G. Thomson of the London School of Hygiene and Tropical Medicine. It is a pleasure to acknowledge Dr. Thomson's kindness and to thank the members of the staff of the London School for the opportunity to study there for several months, during tenure of a fellowship of the John Simon Guggenheim Memorial Foundation.—J. T. C.

TABLE I.—*Demonstrating the resistance to reinfection of young adult rats after recovery from an infection with* Trypanosoma cruzi

	Young adult rat number	Total number of trypanosomes observed in 50 high-dry fields of the microscope on the designated days after the initial injection or after the reinjection with *Trypanosoma cruzi.*																	
		14	16	17	19	20	21	22	26	29	30	32	34	37	40	45	50	55	60
Inital injection 10/21	1	0	0	1	3	2	1	2	3	2	5	2	0	0	0	0	1	0	0
	2	0	0	0	0	1	1	1	4	4	4	2	5	1	1	0	0	0	0
	3	0	0	1	1	5	3	3	3	3	10	2	6	1	1	2	0	1	0
Reinjection 1/18	1	0	0	0	0	0	0	0	0	0	0	0	0	0					
	2	0	0	0	0	0	0	0	0	0	0	0	0	0					
	3	0	0	0	0	0	0	0	0	0	0	0	0	0					
Young adult normal rats (Control for infectivity of suspension used 1/18)	4	0	0	0	0	0	0	8	13	21	2	0	0						
	5	6	6	0	0	11	15	20	59	15	0	Dead							

b. *Passive transfer of immunity against* Trypanosoma cruzi *in rats.* For the work on passive transfer of immunity against *Trypanosoma cruzi* in rats, litters of normal albino rats only 10 to 15 days old when infected were used. Animals of this age had been found previously to show relatively short prepatent periods and to suffer severe and frequently fatal infections with this parasite. The young rats were injected with a standard suspension of infected rat blood which had been citrated and diluted with normal rabbit serum so that from two to three trypanosomes were present in each field of the microscope, using 440 times magnification.

The immune serums were taken from albino rats within a few days after these had recovered from relatively severe infections. These rats ranged from 10 to 30 days of age when they had been infected and, at the time their blood was drawn after recovery, were from 45 to 65 days old.

The serum from rats recovered from *T. cruzi* infection was tested for both prophylactic and therapeutic action, first the effect of a single injection, and, later, the effect of repeated injections being studied. The single prophylactic injection (0.5 cc) was given subcutaneously simultaneously with the intraperitoneal injection of the trypanosome suspension. The single therapeutic injection (0.5 cc) was given on the fifteenth day after the rats had been infected, at a time when trypanosomes were numerous in the blood and were increasing rapidly. The animals which were given multiple prophylactic injections received 1.0 cc of antiserum at the same time as the infecting dose and 0.5 cc on the second, fifth, and seventh days thereafter. The animals given multiple therapeutic injections received 0.5 cc of serum on the twelfth day, when parasites were numerous in the blood, and on the fourteenth, sixteenth, eighteenth, and twentieth days of the infection. Control injections consisted of normal rat serum, which was obtained from normal adult albino

Table 2.—*Action of specific and non-specific antiserums upon* Trypanosoma cruzi *infection in young rats*

Rat No.	Serum injected	Total number of parasites in 50 high-dry fields of the microscope on the designated days after infection																			
		9	12	13	14	15	16	17	19	21	22	23	24	27	28	29	32	33	35	42	56
1–433	0.5 cc anti-*cruzi* rat serum given to each on day of infection	0	0	0	0	0	2	0	0	0	2	6	5	3	5	12	19	15	37	6	0
2–433		0	1	0	0	1	0	0	5	2	5	8	3	54	62	84	114	445	302	Dead	
3–438		0	0	1	0	8	3	2	5	10	42	31	34	91	40	42	19	1	8	0	
4–438	0.5 cc anti-*lewisi* rat serum given to each on day of infection	0	16	9	50	92	155	344	516	790	405	315	257	75	65	54	46	7	2	1	2
5–438		0	25	17	62	39	155	146	344	498	470	370	525	672	2500	Dead					
6–438		0	30	105	240	109	310	325	481	706	Dead										
7–433	0.5 cc normal adult rat serum given to each on day of infection	0	3	1	8	11	36	38	50	86	170	55	35	36	32	17	3	0	0	0	2
8–433		0	1	2	10	11	42	79	47	105	205	92	50	17	1	1	0	0	0	0	0
9–433		0	35	26	42	101	105	236	281	770	870	340	232	230	157	120	44	1	4	0	0
10–433	0.5 cc anti-*cruzi* rat serum given on fifteenth day after infection*	0	25	30	21	46*	7	10	77	42	52	51	45	3	1	1	0	1	0	0	0
11–438		0	12	23	42	90*	3	33	40	350	1410	1420	302	1250	575	240	70	Dead			
12–438		0	50	22	37	112*	3	4	12	8	54	22	14	0	2	1	1	0	0	0	0
13–433	No serum given at any time	0	8	5	13	52	86	114	224	255	345	96	510	370	700	96	87	134	51	0	0
14–433		0	10	20	10	22	46	60	98	100	232	185	82	67	117	97	14	5	8	2	0
15–438		0	30	20	165	200	220	120	282	Dead											

The rats included in this table belong to two litters, numbers 433 and 438.

rats, and anti-*Trypanosoma lewisi* serum, from adult rats recently recovered from *Trypanosoma lewisi* infection.

As a result of the work just described (Table 2) it was found that animals which were given a single prophylactic injection of the serum of rats recovered from an infection with *Trypanosoma cruzi* showed somewhat longer prepatent periods than control animals and, during the first three weeks after infection, the course of the disease in them was irregular and decidedly less severe than in the controls. The administration of normal rat serum or of serum from rats recovered from infection with *Trypanosoma lewisi* failed to influence the course of the infection with *Trypanosoma cruzi,* compared with that of untreated control rats. Following the third week after injection, however, the disease became increasingly severe in the animals which were given one prophylactic injection of anti-*Trypanosoma cruzi* serum, and, although in most cases the infection never became so intense as in animals not so treated, death was recorded for one animal. In those rats given repeated prophylactic injections of anti-*Trypanosoma cruzi* serum (Table 3), the infection in the first three weeks was likewise of very low grade, as shown by examination of the peripheral blood. After the third week, in these animals also, the infection mounted in intensity, although no animal experienced a severe infection and death occurred in no instance.

The anti-*Trypanosoma cruzi* serum was less efficacious in the therapy than in the prevention of *Trypanosoma cruzi* infection. Rats given a single injection of serum 15 days after infection (Table 2), when parasites were numerous in the blood stream, experienced a sharp decrease in the intensity of the blood stream infection, but usually the parasite count began to mount as early as the second or third day thereafter, when apparently the concentration of the injected serum had dropped below an effective value in the blood of the recipient animal. When this experiment was repeated, using a series of serum injections begun after onset of the patent period (Table 3), a similar crisis in the parasite number was noted in every animal and, so long as the serum injections were continued, the parasites showed only a very slight increase in number in the blood. Nevertheless, in no case was cure effected, and three of four rats so treated succumbed on the twentieth day after infection. The fourth animal of this group, given no serum after the twentieth day of the infection, experienced a decided relapse subsequently, the parasite counts rising above the previous peak for that animal.

DISCUSSION

A number of points brought out in the data deserve emphasis. In the first place, recovered rats were wholly resistant to reinfection with *Trypanosoma cruzi.* No parasites at all were seen after their reinjection

TABLE 3.—*The effect of multiple prophylactic and therapeutic injections of specific antiserums upon* Trypanosoma cruzi *infection in rats*

Rat No.**	Serum injected	Total number of parasites in 50 high-dry fields of the microscope on the designated days after infection																	
		7	9	12	14	16	18	20	22	24	26	28	30	33	35	37	39	42	44
1–440	Anti-*cruzi* rat serum given: 1.0 cc on day of injecting trypanosomes & 0.5 cc on 2nd, 5th, 7th days subsequently.	0	0	0	1	0	0	2	2	4	10	10	3	8	3	0	0	0	0
2–440		0	0	0	0	1	0	1	0	2	4	0	1	0	0	0	0	0	0
3–440		0	0	0	0	0	0	3	10	6	12	10	20	7	1	0	0	0	0
4–440	Anti-*cruzi* rat serum given: 0.5 cc on 12th, 14th, 16th, 18th and 20th days after injecting trypanosomes.*	0	51	132*	21*	22*	42*	51*	82	107	146	186	168	72	30	30	10	1	1
5–440		0	115	241*	16*	48*	60*	93*	Dead										
6–440		0	101	244*	17*	60*	121*	272*	Dead										
7–440		0	52	165*	156*	270*	234*	285*	Dead										
8–440	No serum given at any time.	0	59	232	409	467	614	589	1042	Dead									
9–440		0	47	205	361	583	1311	Dead											
10–440		0	0	255	241	479	629	Dead											

** The rats included in this table all are of one litter, number 440.

into the recovered rats, although these rats were examined during twice the number of days of the prepatent period after the initial injection. The young adult animals used in this part of the work had a very considerable natural resistance to this parasite, the initial infections in them being very mild. The subsequent work upon passive immunity was done with much younger rats, these being found normally to experience decidedly more severe infections with this parasite.

The work upon passive immunity indicated that it is impossible completely to prevent or to cure an infection with *Trypanosoma cruzi* by the administration of the specific antiserum. Although the serum succeeded in destroying or at least in depressing the number of the trypanosomes in the blood, it was apparently unable to reach the multiplying forms in the fixed tissues. Therefore, the parasite counts, though temporarily depressed by the injection of antiserum, rose again as the intracellular leishmaniform stages matured and made their way into the circulating blood. Since it is possible that the parasite can maintain itself in an animal exclusively in the intracellular form, without appearing at any time free in the blood, the reason for failure of the antiserum to function more effectively is evident, granting that the action of the serum is confined largely to the blood stream itself. Collier (1931) has indicated that the immunity developed against *T. cruzi* by white mice is dependent upon the continued presence of this parasite in the somatic tissues.

Another point that is well brought out is the failure of the animal to become actively immunized in spite of its infection until the administered immune serum had been eliminated and the infection had attained a considerable severity. Usually, after an interval of three weeks, by which time the influence of the prophylactically injected serum was apparently lost, an acute rise in the intensity of the infection was experienced, the infection curve thereafter being essentially that of a normal animal. A low-grade infection, such as that suffered at the time the injected antiserum was still in the body, was insufficient to initiate an effective immune response in the infected animal. Therefore, after the serum had been lost, the parasites were permitted to multiply largely unchecked.

It may be well to point out the fairly constant appearance of an amber-colored, wax-like substance, resembling the cerumen of the human ear, which characteristically was found upon the lower abdominal wall of the rats heavily infected with *Trypanosoma cruzi*. Those rats which were given prophylactic injections of antiserum showed no such excretion, perhaps since the infection in them never assumed great intensity. The material which under microscopic examination appeared as a purely amorphous mass, could be found only after the blood stream invasion

had become well established. The substance seemed to be excreted through the kidneys with the urine, accumulating until a crusty deposit formed on the hair of the abdomen. This material may be related to the foreign protein of the parasite body or to the metabolic products of the parasite life in the host. In either case, one of the major routes by which the body would attempt to remove this foreign substance from the blood stream is the kidneys. However, we have not observed a similar excretion in rats infected with *Trypanosoma lewisi,* even though in these infections much larger numbers of parasites occur in the blood.

Another symptom noted frequently in animals which died of their infections was a flaccid paralysis of the hind-legs. This was seen only in those animals which suffered a heavy infection and in none of those which were given prophylactic injections of specific antiserum. It is possible that these symptoms are explained by the observations of Crowell (1923) who reported evidence of kidney damage and invasion of the nervous system in *Trypanosoma cruzi* infections. Finally, in the severe infections there was a characteristic failure of animals to grow and increase in weight normally.

In closing this paper, it should be mentioned that the rat, like man, is an abnormal host for *Trypanosoma cruzi,* the natural vertebrate reservoir for this parasite being the armadillo. Yet the fact that these animals —man and rat—both are abnormal hosts seems to make possible the application of results arrived at through the study of this infection in rats to the human disease. The course of the infection (Regendanz, 1930) and many of the symptoms elicited by infection are apparently similar in the two species. It was in the hope that an investigation of the immunity which rats develop through infection with this parasite would throw some light upon the immunology of the human disease that the present study was undertaken.

CONCLUSION

Rats which have recovered from an infection with *Trypanosoma cruzi* are insusceptible to reinfection with this parasite. The serum of rats recovered from infection with *Trypanosoma cruzi* confers protection to normal rats on injection to these animals. Although administration of the serum prophylactically does not completely prevent infection with the parasite, it generally permits development of only a low-grade or aborted type of infection. Given therapeutically, the serum causes an incomplete crisis in the number of parasites in the blood stream, but a relapse can be expected very soon after the last of the serum injections has been given. Once the parasites are established in the somatic cells, the serum is apparently unable to reach them to affect their development since its action is probably limited to those forms which invade the blood stream.

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IN MEMORIAM

Harold Benjamin Fantham (1876–1937)

H. B. Fantham, an outstanding parasitologist and zoologist, who combined great research ability with a marked capacity for interesting and inspiring students, passed away on October 26, 1937.

Dr. Fantham held the degrees of M.A., Cambridge (Christ's College), and D.Sc., London (University College). In London he was gold medallist in zoology and Derby research scholar, and in Cambridge was Darwin prizeman. He was a fellow of University College, London.

From 1904 onwards Dr. Fantham was actively engaged in University teaching and research. He held positions at St. Mary's Hospital Medical School and University College, London, at Cambridge, and at the Liverpool School of Tropical Medicine. During the Great War, he was parasitologist first to the Western Command and then in Egypt, Salonika and Malta. In 1917, Dr. Fantham was appointed as the first professor of zoology and comparative anatomy in the new University of the Witwatersrand, Johannesburg, South Africa. Here he organized and built up an outstanding department, founded a school of research, served on the senate of the University, was secretary of the faculty of science for one year, and then for four years in succession was elected by the faculty as dean of the faculty of science, refusing election for a further period. While in South Africa, he was well known as a popular public lecturer on zoological subjects and on eugenics. In 1921 he was president of the zoology section of the South African Association for the Advancement of Science and in 1927 Grand President of that Association. In 1931 he received the 21st award of the South Africa Medal and Grant. The publication of this citation (*South African Journal of Science,* 1931, 28: XXXVI–XLII) includes a bibliography of over 100 of his scientific papers.

In January, 1933, Professor Fantham became Strathcona professor of zoology and head of the department at McGill University, Montreal. Here again he gained an enviable place by his departmental development and teaching, which was reflected in a rapidly growing number of students.

As a research worker Dr. Fantham specialized on the protozoa—parasitic, soil and free-living—and has enriched our knowledge of practically every group. When in England, he did much work on the haplosporidia, human trypanosomes including *Trypanosoma rhodesiense* Stephens and Fantham, herpetomonads, spirochaetes, microsporidia and myxosporidia. In South Africa he made a survey of the parasitic pro-

tozoa of the indigenous fauna, and described a large number of new species of myxosporidia, Protoopalina and herpetomonads from plants. A series of ten papers on soil protozoa formed a comprehensive survey of this fauna of South African soils. Dr. Fantham also published a number of papers dealing with his research on human heredity and race admixture. In Canada, Dr. Fantham continued his researches on protozoa and race admixture. Realizing the enormous almost untouched field in Canada for fresh-water biology, he was beginning the development of this side of ecological zoology.

Dr. Fantham was a most meticulous and logical worker. Besides his numerous research papers (some of which were in collaboration with his wife, Dr. Annie Porter), he wrote the section on protozoa in "Animal Parasites of Man," by Fantham, Stephens and Theobald, a popular book (with Dr. Porter) on "Some Minute Animal Parasites," and articles in various encyclopaedias and popular scientific journals. An artist of considerable ability, musical, a good speaker and excellent lecturer, with extraordinarily wide knowledge and interests, he was greatly loved by his students wherever he taught.

REVIEWS

L'Anophélisme en Extrême-Orient. Contribution faunistique et biologique. By C. Toumanoff. Preface by E. Roubaud. viii + 434 pp., 75 figs. and 20 tables in text. Paris, Masson et Cie. 1936. 60 fr.

This is Monograph IV of the Collection de la Société de Pathologie Exotique of Paris, from the pen of the Chief of the Entomological Laboratory of the Institut Pasteur of Indo-China. It is a faunistic and binomic study over a period of two years of 18 anopheline mosquitoes prevalent in Indo-China. The first chapter gives the procedures in field and laboratory investigations and discusses the basis of classification. The second treats of the anopheline fauna of Tonkin, with briefer references to those of the basin of the Si-Kiang, North Annam, Laos, and Central Indo-China. The author has studied the local distribution, characteristic habitats, and the seasonal distribution throughout the year of the various species. The third chapter deals in like manner with the maritime lowlands of Annam and is concerned mainly with the *rossii-ludlowi* group of species of *Myzomyia* (s. str.).

The fourth chapter deals with the binomics of the several species in Tonkin and in Central Indo-China. The author seeks to give an inclusive picture of the environmental features of both larval and adult stages in their relations to the habits and distribution of these two stages.

The precise epidemiological work of the author reveals *A. minimus* as by far the primary vector, with *jeyporiensis, aconitus, maculatus,* and *vagas* as secondary, although Bevel had placed *A. maculatus* and *A. kochi* under suspicion as chief vectors of the malarial parasite in Central Indo-China. Infected *minimus* occur in diverse localities often widely separated and in varying degrees of incidence from 1.5 to 3.5 per cent in dissected mosquitoes without evidence of correlation with physiographic conditions. Zoophily and abundance of favorable sites are important factors influencing degree of infection. The maximum of sporozoite bearers is found in the winter months or dry season. The highest percentage of infection in *A. maculatus* was 2.3 per cent, a considerable reduction below preliminary findings. *A. vagus* showed 2.3 per cent.

In experimental infection of female mosquitoes the percentage of success does not follow the number of gametes per cubic millimeter of blood, nor do different species fed on the same patient infect equally. There appears to be a factor of receptivity of the individual vector involved in the result of feeding. This non-receptivity is one factor in *anophélisme sans paludisme.* The author devotes a long chapter to the discussion of the relation of the feeding habits of Anopheles to the transmission of the malarial parasite, and follows Roubaud and others, who have suggested and tested by experiment the tropisms of mosquitoes for other animals than man with resulting zoophily as its cause. In experimental attempts to deflect *A. minimus* from man to cattle (ox and buffalo) a deviation of 50 per cent was observed, while with *A. jeyporiensis* the larger part were deflected. With *A. aconitus,* a secondary vector, animal blood was more frequently detected than in the above-named species, especially if stables were near houses. There are thus among different species of mosquitoes degrees of zoophily and anthrophily. Malaria is rare in the delta lands of Indo-China where domestic animals are relatively more abundant than in malarial districts.

The prevalence of zoophily among many of the principal mosquitoes of Indo-China leads the author to suggest experimentation to test the possibility of increasing zoophily in *A. minimus* as an antimalarial measure.

It appears to the reviewer that animal blood may reduce the susceptibility of the mosquito to infection by the malarial parasite, or in some unknown way inhibit fertilization in the mosquito's stomach. It might be rewarding to search the blood of the ox, buffalo, and other domesticated mammals for *Plasmodium* and, if found, to test the relation of the effect of this blood upon the infective process in mosquito and man.—C. A. Kofoid.

Clinical Parasitology. By Charles Franklin Craig and Ernest Carroll Faust. 733 pages, 243 illustrations. Philadelphia, Lea and Febiger, 1937. $8.50.

This book by two well-known parasitologists, a protozoologist, and a helminthologist, is the result of their combined efforts to produce a text not only suitable for practicing physicians but also designed for courses in parasitology in medical schools and for graduate and advanced undergraduate students in courses in parasitology in universities. Since the authors wrote for these groups one should not expect to find any but already published work and this is the case. The material comprises for the most part textual matters and illustrations of previously published texts by these authors, treatment here being more abbreviated, with major emphasis still on the details of morphology, life history, and systematics. Viewed as a new edition of two former books written separately by these authors, there is here the advantage of having the information, with additions, in one volume.

To those unfamiliar with the writings of Craig and of Faust, their style of presentation is clear and accurate and the various species discussed are familiar to them from first-hand knowledge. Sections deal with protozoa, helminths, arthropods technical appendix which includes a list of representative parasites, the international code of zoological nomenclature and official generic names of medical importance, and literature of clinical parasitology. One may find in these sections knowledge of distribution, morphology, life history, epidemiology, pathology, symptomatology, diagnosis, prognosis, treatment, and prevention.

There are minor errors and omissions but these do not discount the general worth of the text. Thus, the date for Donné's discovery of *Trichomonas vaginalis* is 1836 and not 1837 as stated. While Dobell and Wenyon are quoted as believing the Trichomonas species of man are identical, equally careful investigators are not referred to who have maintained on splendid basis that the species are distinct. Another omission of similar nature is made in regard to *Taenia confusa* where Faust omits reference to Anderson's careful study on the validity of this species and his conclusion that the species is not distinct from *Taenia saginata.* The Icelanders will rightly object to the statement that hydatid disease is "most extensive" there, for now only about thirty cases are known in the whole island. The history of the control of hydatid disease in Iceland is a brilliant chapter in parasitology and should not be omitted. Absence of eosinophilia in trichinosis may indicate a very mild infection rather than be a sign of poor prognosis. Unless physicians become cannibalistic it will hardly be necessary to admonish them to guard against infecting themselves at "autopsies of infected cases." If one were inclined to be facetious he might point out that "Clinical Parasitology" is a questionable title since most of the book is devoted to parasitology which is not "bedside," but then, much of parasitology is really not bedside.—T. M. Magath.

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